BIOGEOGRAPHICAL HISTORY OF NORTH AMERICAN WOOD WARBLERS AND THE ASSEMBLY OF THE NORTH AMERICAN AVIAN BIOTA

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ABSTRACT

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Differences in patterns of species richness and taxonomic composition across continents are well documented. However, less is known about how these patterns originate from the fundamental processes that contribute to the assembly of continental biotas: speciation, extinction, immigration, and emigration. To truly decipher how these processes operate at a continental scale, it is crucial to understand how Earth-history events and environmental change shaped the biogeographical history of the taxa occurring in a region.

The Pleistocene glacial cycles have been hypothesized to be a significant geological event which affected the Earth's biota over the past three million years. During this period, multiple cycles, in which ice sheets covered a large portion of the Northern Hemisphere, have been hypothesized to facilitate allopatry and ecological differentiation. The central goal of this dissertation is to understand the assembly of continental biotas by integrating the role of Earth's geological and environmental history and recent (late Quaternary) changes in distributions.

Here, I studied the North American wood-warblers, which are passerine birds belonging to the family Parulidae. In the first chapter of this dissertation, I examined the extent to which recent diversification is underestimated by ignoring recently diverged taxa. To do so, I evaluated the effect of taxonomic delimitation on the inferred temporal patterns of diversification of wood-warblers in the genus *Setophaga*. My results show that species-level taxonomic delimitation in ecological and evolutionary studies is crucially important but is often ignored. Evaluating the effect of taxonomic delimitation in the genus *Setophaga* is particularly relevant because it has been widely cited as an ideal example of niche saturation, and previous studies suggested that lineages in this particular radiation exhibited an asymptotic accumulation of diversity through time. In this chapter, however, I demonstrate that this pattern was likely a consequence of the ways in which taxonomic diversity was sampled.

In the second chapter, I examined how biotic and abiotic factors limit the distribution of species of the genus *Oreothlypis* at a continental scale. For most of the taxa examined, climatic- and biotic-based areas of suitability were equivalent, and therefore the relative importance of these factors could not be disentangled. However, in some cases, biotic variables limited the distribution in areas climatically suitable, and vice versa. The results of this chapter highlight the importance of considering potential effects of biotic interactions in the study of climate-driven range shifts. This paper is also an important methodological contribution to the general field of ecological niche modeling (ENM) by integrating climatic and palynological data to empirically estimate both abiotically and biotically suitable areas which that has only been done theoretically so far.

In the third chapter, I integrated phylogenetic data, biotic and climatic ENMs, and reconstructions of environments during the LGM to test how cycles of fragmentation, differentiation, and expansion during the Pleistocene shaped the biogeographical patterns of the genus *Oreothlypis* in North America. Based on a time-calibrated phylogeny I identified two groups of taxa that diversified during the last million years and therefore were potentially affected by glacial cycles. My analyses suggest that there were rapid switches in the environmental conditions in which species of the genus occur and that glacial cycles resulted in dramatic range shifts from glacial maxima to interglacials. Distribution patterns during the LGM suggest that divergence in areas isolated by glaciers presumably contributed to the geographical structuring of *Oreothlypis*, as well as to their taxonomic and ecological diversity in the present.

In summary, this work illustrates how wood-warblers are an ideal model system for examining the large-scale history of the North America biota and environment, particularly over the Pleistocene. They are highly diverse, have endemics in virtually all of North America's areas of endemism and ecosystems, and many of these patterns are repeated within and across clades. Furthermore, distributional patterns in warblers show high congruence with those of other organisms; thus inferences made about the history of this group likely have implications for understanding the biotic history of North America in general. In addition, many warblers have narrow ecological preferences in that they occupy forest environments with specific tree compositions. As a consequence, ecological models of their distributions, integrated with the North

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INTRODUCTION

Differences in patterns of species richness and taxonomic composition across continents are well documented (Willig et al. 2003). Often, climatic conditions in the present (Hawkins et al. 2003) and past (Graham et al. 2006) are correlated with the number of species present in an area, and limit the occurrence of certain groups of vertebrates (Kozak and Wiens 2010b; Wiens et al. 2006). However, less is known about how these patterns originate from the fundamental processes that contribute to the assembly of continental biotas: speciation, extinction, immigration and emigration (Jablonski et al. 2006; Wiens 2011; Wiens and Donoghue 2004). To truly decipher how these processes operate at a continental scale, understanding the biogeographical history of the taxa occurring in the region is crucial.

The origin of the North American biota is complex and has been affected by historical factors that span long periods of time, including connections with other continents (Sanmartin et al. 2001; Smith and Donoghue 2010), orographic activity (Calsbeek et al. 2003; Pitts et al. 2010) and climate change (Cronin 2010). In particular, the Pleistocene glacial cycles, during which ice sheets covered a large portion of the continent (Ehlers and Gibbard 2004) have been hypothesized to have been important for North American biota. These climatic fluctuations drove sequential expansions

and contractions of the geographical distributions of species (Hill et al. 2011; Holt 2009), which facilitated allopatry and differentiation during glacial maxima (Mengel 1964; Shafer et al. 2010; Soltis et al. 2006).

While it is well documented that the distributions of species shifted during the glaciations (Hewitt 2000), there is still controversy over the importance of the Pleistocene glacial cycles in the formation of extant species (Lovette 2005). If speciation during glacial cycles was particularly important in generating diversity in temperate regions, clades distributed in latitudes affected by glaciations should have an increase in diversification rates during the Pleistocene, giving rise to a greater number of species during this period. This prediction has been examined in North American birds with contrasting conclusions. On one hand, Weir and Schluter (2004) found a strong latitudinal gradient in the ages of speciation events: boreal taxa originated during the Pleistocene while Neotropical species tended to be older. Similarly, Johnson and Cicero (2004) estimated that a high proportion of species originated during the last 500 Ka. These two studies contrast with those of Zink et al. (2004) and Zink and Klicka (2006) who concluded that both diversification rates and the proportion of species that originated during the Pleistocene did not differ from a null model of constant diversification. These studies likely underestimate the importance of recent diversification by including only biospecies, excluding slightly

differentiated forms (Zink et al. 2004). Furthermore, the studies mentioned above focused on particular pairs of sister taxa and their current distributions, but overlooked the biogeographical history of the lineages. The central goal of this dissertation is to understand the assembly of continental biotas by integrating the role of Earth's geological and environmental history and recent (late Quaternary) changes in distributions.

To do so, I studied the North American wood-warblers, which are passerine birds belonging to the family Parulidae. Since the separation from its sister clade about 11 Ma (Barker et al. 2013; Cracraft and Barker 2009), the family has diversified into about 115 species distributed across a wide variety of habitats in the Americas, with 49 species breeding in North America (Curson 2010), 36 of which belong to two genera with relatives in the Neotropics: *Setophaga* and *Oreothlypis* (sensu Lovette et al. 2010). The phylogenetic relationships among biospecies in the family are well understood (Lovette et al. 2010), which provides an important baseline for further phylogenetic and biogeographical studies. Additionally, warblers, particularly those in North American, have been used as model organisms for both ecological (Macarthur 1958; Shutler and Weatherhead 1990) and community assembly (Lovette and

Hochachka 2006) theories, as well as biogeographical and evolutionary studies (Mengel 1964; Rabosky and Lovette 2008a).

To understand the extent to which recent diversification is underestimated by ignoring recently diverged taxa, I evaluated the effect of taxonomic delimitation on the inferred temporal patterns of diversification of wood-warblers in the genus *Setophaga*. The first chapter of this dissertation addressed how species-level taxonomic delimitation in ecological and evolutionary studies is crucially important but is often ignored. I showed that conclusions inferred from these studies—in this case, regarding diversification rates— are often sensitive to the criteria used to delimit and sample these units. Evaluating the effect of taxonomic delimitation in the genus *Setophaga* is particularly relevant because it has been widely cited as an ideal example of niche saturation; and previous studies suggested that lineages in this particular radiation exhibited an asymptotic accumulation of diversity through time (Rabosky and Lovette 2008a). In this chapter, however, I show that this pattern was a consequence of the ways in which taxonomic diversity was sampled.

In the second chapter, I examined how biotic and abiotic factors limit the distribution of species of the genus *Oreothlypis* at a continental scale. For most of the taxa examined, climatic- and biotic-based Ecological Niche

Models were equivalent, and therefore the relative importance of these factors could not be disentangled. However, in some cases, biotic variables limited the distribution in areas climatically suitable, and vice versa. The results of this chapter highlight the importance of considering potential effects of biotic interactions in the study of climate-driven range shifts. This paper is also an important methodological contribution to the general field of ecological niche modeling by integrating climatic and palynological data to empirically estimate both abiotically and biotically suitable areas which that has only been done theoretically so far.

In the third chapter, I integrated phylogenetic data, biotic and climatic ENMs, and reconstructions of environments during the LGM to test how cycles of fragmentation, differentiation, and expansion during the Pleistocene shaped the biogeographical patterns of the genus *Oreothlypis* in North America. Based on a time-calibrated phylogeny I identified two groups of taxa that diversified during the last million years, and therefore were potentially affected by glacial cycles. My analyses suggest that there were rapid switches in environmental associations among species of the genus, and that glacial cycles resulted in dramatic range shifts from glacial maxima to interglacials. Distribution patterns in *Oreothlypis* during the LGM were broadly congruent with those from other studies in the continent (Roberts and Hamann 2015; Shafer et al. 2010; Weir and

Schluter 2004), and divergence in areas isolated by glaciers and ecologically unsuitable habitats presumably contributed to the geographical structuring of taxonomic diversity of these warblers in the present.

In summary, the three chapters outlined above illustrate how wood-warblers are an ideal model system for examining the large-scale history of the North America biota and environment, particularly over the Pleistocene. They are highly diverse, have endemics in virtually all of North America's areas of endemism and ecosystems, and many of these patterns are repeated within and across clades. Furthermore, distributional patterns in warblers show high congruence with those of other organisms; thus inferences made about the history of this group likely have implications for understanding the biotic history of North America in general. In addition, many warblers have narrow ecological preferences in that they occupy forest environments with specific tree compositions. As a consequence, ecological models of their distributions, integrated with the North American pollen record of forest change, provide a new perspective on ecosystem change during glacial cycles, and its impact on the origin and maintenance of biodiversity in the continent.

1. IS DIVERSITY-DEPENDENT DIVERSIFICATION IN *SETOPHAGA* WARBLERS AN ARTIFACT OF SPECIES DELIMITATION?

1.1. INTRODUCTION

Multiple studies examining the temporal patterns of diversification have found that lineages accumulate at a faster rate at the beginning of a radiation with a subsequent decline in rate, resulting in an asymptotic accumulation curve (Moen and Morlon 2014; Rabosky 2013). This pattern has been hypothesized to be a consequence of diversity-dependent diversification, in which ecological opportunities for the newly formed taxa are progressively saturated, reducing the rates of speciation or increasing extinction (Glor 2010; Phillimore and Price 2008; Rabosky 2013; Schluter 2000). However, studies demonstrating a mechanistic explanation of how ecological saturation might affect these rates have been questioned (Moen and Morlon 2014).

A prominent example of presumed diversity-dependent diversification is the radiation of wood-warblers of the genus *Setophaga* in North America (Rabosky and Lovette 2008a). This group has often been presented as an ideal example of niche partitioning because several species of the genus occur in sympatry where they differ in subtle aspects of their foraging and

breeding behavior (Macarthur 1958; Price et al. 2000; Rabosky and Lovette 2008a). Rabosky and Lovette (2008a) used a molecular phylogeny to examine variation in rates of diversification across time for this group, finding a significant slowdown in diversification rates, which they argued was consistent with the saturation of ecological opportunities being the significant factor influencing the pattern (Rabosky and Lovette 2008a).

Multiple studies have demonstrated the potential problems associated with analyses of diversification rates using molecular phylogenies (Morlon 2014; Rabosky 2013). Rabosky and Lovette (2008a), in particular, addressed the possible effect of incomplete taxon sampling on their findings, concluding that results would hold even if the sample represented as little as 25% of the taxa in a clade with a constant rate of diversification. More generally, research has focused on the impact of tree reconstruction (Revell et al. 2005; Ruane et al. 2014), gene-tree species-tree discordance (Burbrink and Pyron 2011), the difficulties discerning the effects of extinction (Bokma 2009; Rabosky 2010; Rabosky and Lovette 2008b), and incomplete taxon sampling when it is both random (Cusimano and Renner 2010; Pybus and Harvey 2000; Rabosky and Lovette 2008a) or clade-biased (Brock et al. 2011).

Importantly, however, the effect of the taxonomic units used in diversification rate analyses has received little attention, and while in theory it has been recognized that incomplete sampling due to unrecognized intraspecific taxa would result in an artificial slowdown in the rates of diversification (Purvis et al. 2009; Weir 2006), terminal taxa in most studies are still “biospecies” (species delimited under the biological species concept), which exclude from the analyses taxonomic diversity within these units (but see d'Horta et al. 2013; Smith et al. 2013b). This is particularly relevant in cases like the radiation of *Setophaga* in that multiple biospecies of the radiation are polytypic (Curson 2010), suggesting significant taxonomic diversity is present, which is often recognized at the subspecific level (e.g. Boulet and Gibbs 2006; Cháves et al. 2012; Milá et al. 2007). Complicating matters, some biospecies of *Setophaga* have been shown to be paraphyletic (Lovette and Bermingham 2001), and multiple recent studies propose the elevation of several subspecies to biospecies (Brelsford and Irwin 2009; Evans et al. 2014; Mckay et al. 2010; Milá et al. 2007). In contrast, patterns recovered from analyses using evolutionary taxa (phylospecies) more accurately reflect the results of the processes of cladogenesis (d'Horta et al. 2013; Losos and Glor 2003; Smith et al. 2013b; Wiens 2004b). Additionally, even when controlling for random or clade-biased incomplete sampling, ignoring these taxa may result in a bias towards an asymptotic accumulation of

lineages. (Etienne and Rosindell 2012; Purvis et al. 2009; Smith et al. 2013b).

To test the importance of taxonomic delimitation on temporal patterns of diversification in *Setophaga* wood-warblers, I sampled multiple individuals of all North American named taxa and most of the Neotropical ones. This information allowed us to identify potential phylospecies within the clade, and perform diversification-rate analyses contrasting the results of three different sets of terminal taxa (Table 1.S1): (1) the paraphyletic group used by Rabosky and Lovette (2008a) of 25 taxa representing only North American biospecies of *Setophaga* (minus all Caribbean taxa), (2) 30 biospecies of the North American radiation including five taxa that secondarily recolonized the Caribbean , and (3) 43 taxa including all recognized phylospecies of the 30 biospecies in the second analysis. Additionally, I contrast the empirical results with those obtained by simulations of incomplete taxon sampling, both random and biased towards missing, recently-diverged taxa. The results suggest an important effect of taxonomic delimitation on the temporal patterns of diversification in this group and highlight the importance of including all taxonomic diversity in diversification analyses.

1.2. METHODS

1.2.1. Sampling and Phylogenetic Analyses

I analyzed a total of 179 individuals from *Setophaga* (sensu Lovette et al. 2010; Table 1.S1). This clade includes a total of 34 biospecies and 115 named taxa. For 20 monotypic biospecies I used previously published data (Lovette et al. 2010; Rabosky and Lovette 2008a) including nuclear and mitochondrial loci. For polytypic species, I used subspecies as a proxy for phylospecies (assuming that the diagnosis of the subspecies had geographical and morphological bases; Remsen 2010). Because not all named forms are currently considered valid taxa, and most of them have not been evaluated since their description (Remsen 2010), I controlled for a possible effect of over-splitting in the results by taking a conservative approach and lumping dubious taxa (i.e. those not recognized as subspecies in Curson (2010) or more recent and detailed studies). Four early branching Caribbean species of the *Setophaga* (*S. bishopi*, *S. plumbea*, *S. angelae* and *S. pharetra*) which are the closest relatives (Lovette et al. 2010) to clade analyzed by Rabosky and Lovette (2008a) were used in this study as outgroups.

I sampled multiple individuals per subspecies and sequenced the

mitochondrial cytochrome *b* and ND2 loci following methods described in Lovette et al. (2010). I reconstructed the relationships among these individuals based on maximum likelihood as implemented in GARLI 2.0 (Zwickl 2006) on the CIPRES portal (Miller et al. 2010) and evaluated node support with 500 bootstrap replicates. I identified phylospecies by taxonomic and geographical congruence as well as diagnosability in mtDNA, recognizing a total of 43 phylospecies. Importantly, for cases in which intraspecific phylogeographical structure was present, but only one individual per subspecies was sampled, phylospecies were defined conservatively disfavoring over-splitting, and thus represent an underestimate of the taxonomic diversity (see results for details). Therefore, the bias introduced in the analyses by my taxonomic delimitation is in the same direction as using biospecies. For those phylospecies not equivalent to monotypic species, and thus not previously sequenced, I sequenced four nuclear markers, including Rhodopsin intron 1 (Rho1), myoglobin intron 2 (Myo2), muscle-specific tyrosine kinase intron 4 (Musk4) and aconitase 1 intron 9 (Aco9) using the same set of primers referenced by Rabosky and Lovette (2008a).

I estimated a phylogeny for all phylospecies by performing Bayesian analyses in BEAST 1.8 (Drummond and Rambaut 2007). To compare my results with those previously published (Rabosky and Lovette 2008a), I

used an uncorrelated lognormal relaxed-clock model, obtaining ultrametric trees calibrated to a relative timescale (the root of the trees were scaled to 1.0). To assess convergence in the Bayesian analyses, I performed five independent runs of 100 million generations each with a GTR+G model of sequence evolution and using default priors with the exception of the parameters of the substitution matrix, for which uniform [0, 100] priors were set (Rabosky and Lovette 2008a) and used a 15% cut-off for the burn-in. I ran the analyses with the biospecies and phylospecies datasets independently, and pruned out the Caribbean taxa from the biospecies trees to obtain the same set of taxa as Rabosky and Lovette (2008a).

1.2.2. Diversification Rate Analyses

To examine variation in diversification rates through time, I based all my analyses on 5000 randomly selected trees for each set of terminal taxa from the resulting BEAST distribution of trees. I used lineage through time (LTT) plots to visualize the temporal variation in accumulation of lineages and computed the Pybus and Harvey (2000) gamma statistic; gamma values significantly lower than 0 imply a slowdown of diversification rates.

The power of gamma statistics to detect diversity-dependent decrease in diversification rates have recently been questioned (McPeek 2008),

therefore, I also compared the fit of the resulting BEAST trees to five models of diversification as implemented in the Laser package v2.4 (Rabosky 2006a). Two of these models had a constant rate of diversification: (I) a pure-birth model (PB; Yule 1924) and (II) a birth–death model, (BD; Kendall 1948; Nee et al. 1994); and three other models had a variable diversification rate: (III) a variant of the pure-birth-model in which there is one shift of diversification rate (yule2rate; Rabosky 2006b), (IV) a diversity-dependent model that assumes an exponential decline in speciation rate with diversity (DDX; Nee et al. 1992; Rabosky 2006b), and (V) a logistic-variant of the diversity-dependent model (DDL; Nee et al. 1992; Rabosky 2006b). Based on the AIC scores of these models, I estimated the probability of either DDX or DDL being the best model, given the data and the model set (Anderson 2008). To test whether the patterns recovered are consistent with diversity-dependent diversification under a non-zero extinction rate, in addition to the models above, I fitted the MCC trees for each of the date sets to a DDL+E model using the R package DDD version 3.0 (Etienne et al. 2012).

1.2.3. Incomplete Sampling Simulations

To evaluate the effect of incomplete taxon sampling on the gamma statistic and the probability of diversity-dependent models, I created

incomplete trees pruning the MCC trees of biospecies and phylospecies. I generated 1000 trees for each number of terminal taxa from 15 to the complete tree (30 for the biospecies and 43 for the phylospecies tree) under two scenarios: (I) random incomplete sampling, in which every tip had the same probability of not being included in the tree and (II) incomplete sampling in which the probability of a terminal taxon being dropped was inversely proportional to the length of the terminal branch leading to it. All calculations, tree manipulation and visualization were performed in R 3.1.1 (Team 2014) and the APE (Paradis et al. 2004), GEIGER (Harmon et al. 2008) and PHYLOCH (Heibl 2008) packages.

1.3. RESULTS

1.3.1. Phylogenetic Analyses

The maximum likelihood tree of all individuals sampled for mtDNA (Fig. 1.S1) resulted in relationships congruent with those of Rabosky and Lovette (2008a) and Lovette et al. (2010). Except for two cases, monophyly of all biospecies was well supported by mtDNA. First, in agreement with previous studies (Evans et al. 2014; Lovette and Bermingham 2001), the Tropical Parula (*Setophaga pitiayumi*) was paraphyletic, with South American subspecies being more closely related to the American Parula (*S. americana*) than to the North and Central American forms. Second, the Golden-cheeked Warbler (*S. chrysoparia*) was nested within Black-throated Green Warbler (*S. virens)*, which is consistent with the traditional treatment of these forms being close relatives (Curson 2010; Mengel 1964; Rising 1988).

I delineated 43 phylospecies based on groupings of named taxa diagnosable with mtDNA. Three particular cases in which I favored lumping taxa to avoid the effect of over-splitting in the analyses are worth noting. (I) The Tropical Parula (*S. pitiayumi*), despite comprising 14 subspecies and a great amount of phylogeographical structure, only three

lineages were treated as phylospecies: *S. p. pitiayumi* (South American subspecies), *S. p. nana* (Central and North American subspecies), and S. *p. graysoni* (from Socorro Island; Evans et al. 2014). (II) Yellow-rumped Warbler (*S. coronata*), in which North American subspecies were treated as one taxon because they are indistinguishable using mtDNA (Milá et al. 2007) even though they are phenotypically distinct and possibly reproductively isolated (Brelsford and Irwin 2009). (III) the Yellow Warbler (*S. petechia*) for which 44 subspecies have been described. Because this likely represents a case of over-splitting, I lumped them into three geographically non-overlapping and morphologically diagnosable groups (Curson 2010; Curson et al. 1994).

1.3.2. Diversification Rate Analyses

The multi-locus ultrametric Maximum Clade Credibility (MCC) tree from BEAST (Fig. 1.1), using one individual for each of the phylospecies, was congruent with the mtDNA and previously published ones (Lovette et al. 2010; Rabosky and Lovette 2008a). Lineage-through-time (LTT) plots (Fig. 1.2a) suggested a non-constant rate of diversification for the three sets of terminal taxa. Whereas all three of them appeared to have slower rates towards the present, only the accumulation curves of North

American biospecies (Rabosky and Lovette 2008a) and all biospecies (black and red in Fig.1.2a, respectively) seemed to be asymptotic.

To test whether the diversifications rate patterns depicted by the LTT plots were significant, I calculated the gamma statistics for the MCC tree of each set of taxa. For both sets, North American taxa and all biospecies, gamma were negative (-3.28 and -3.04, respectively) and significantly different from 0, consistent with a slowdown of diversification rates with time. Moreover, the distribution of the gamma statistic of all sampled trees of the BEAST analyses almost completely overlapped (Fig. 1.2b red and black). In contrast, gamma for the MCC tree of phylospecies was negative (-0.49) but not significantly different from 0, thus a constant rate of diversification could not be rejected.

Similarly, for the likelihood-based analyses, diversity-dependent models of diversification were the best fit to the data for the sets of taxa including only biospecies, whereas a model with two constant rates was the best fit for the dataset of phylospecies. For the maximum clade credibility tree from the BEAST analysis, the probability of either a linear or exponential model of diversity-dependent diversification being the best fit to the biospecies set of taxa from North America was 70% and was 79% across the set of all species. In contrast, the average probability across the

phylospecies trees was only 3% (Fig.1.2c). When including a diversity-dependent model accounting for non-zero extinction, this pattern holds and the probability of any diversity-dependent model was 77%, 86% and 16% for the North American biospecies, all biospecies and phylospecies MCC trees respectively.

1.3.3. Incomplete Sampling Simulations

The simulation analyses designed to understand the effect of incomplete sampling on the gamma statistic (Fig. 1.3) as well as the likelihood-based probability of diversity-dependent models being the best fit to the data (Fig. 1.S2) produced similar results. When incomplete sampling was random (Fig. 1.3a), the tendency of the gamma values for the simulated incomplete trees depended on whether the starting tree was the phylospecies or the biospecies dataset. Gamma in the trees using phylospecies became more negative as missing taxa increased; however, 90% of the iterations did not show a significant slowdown for trees with more than 21 taxa (thus, less than 51% missing taxa). Importantly, the simulated trees were not significantly different from zero when the number of taxa was equal to the number of biospecies, suggesting that random incomplete sampling alone cannot account for the slowdown inferred from the complete biospecies tree. The simulation starting from the biospecies

tree showed on average an increase in gamma. The value calculated for the tree with only North American biospecies was close to the average of the simulations based on the biospecies tree for the same number of taxa, and within 90% of the simulated values, suggesting that in this case the exclusion of Caribbean species by Rabosky and Lovette (2008a) did not have an important effect on their analyses.

Simulations using both the phylospecies and biospecies trees in which incomplete sampling was biased towards leaving out younger taxa, resulted in gamma becoming increasingly more negative as the number of taxa was reduced in simulations (Fig. 1.3b). When the simulations based on the phylospecies phylogeny had the same number of taxa as the other datasets, the empirical value of gamma for both trees (biospecies and North American biospecies) was close to the mean of the simulations. This implies that sampling taxa only based on their divergence time has the same effect as limiting the analyses to biospecies, which are defined by putative reproductive isolation.

1.4. DISCUSSION

I found important differences in the patterns of temporal variation of rates of diversification depending on the taxonomic framework in which these analyses are performed. Specifically, I show that ignoring taxa within traditional biological species created asymptotic LTT plots. This apparent slowdown in diversification rates was significantly more marked than that obtained by random incomplete sampling (Fig. 1.3a) but indistinguishable from incomplete sampling of recently diverged taxa (Fig. 1.3b), a factor that has been shown to have little correlation to reproductive isolation (Coyne and Orr 2004; Rabosky and Matute 2013). These results are consistent with the fact that avian species are often recognized by divergence in morphological or behavioral characters (Sangster 2014) and not by a direct assessment of reproductive isolation (Gill 2014); longer divergence times allow more of such characters to evolve. Additionally, taxonomic changes in this group, and broadly in North American birds, are shifts in rank and not new taxon descriptions (e.g. in Setophaga: Brelsford and Irwin 2009; Evans et al. 2014; Mckay et al. 2010; Milá et al. 2007). Therefore, patterns derived from phylospecies, and the conclusions drawn from them, will be less likely to depend on the taxonomic *status quo* and therefore be more stable, in particular in well-known taxa and regions.

Practical limitations of the biological species concept notwithstanding, different sets of taxa led to discordant temporal patterns of diversification of the same radiation. Therefore, it is not trivial to question the criteria used to delineate terminal taxa and how they relate to the mechanisms behind diversification. This study adds to the body of work highlighting the importance of species delimitation in the study of speciation, which has been posed from a theoretical point of view (Cracraft 1983; Wiens 2004b), tested with paleontological data (Ezard et al. 2012) and molecular phylogenies (Smith et al. 2013b). The lag between the formation of a new taxon and the evolution of reproductive isolation (Coyne and Orr 1997; Etienne and Rosindell 2012), or the characters used to detect it, creates an artificial decrease in the inferred diversification rate (Purvis et al. 2009). Moreover, terminal taxa in most molecular phylogenetic studies are based on biospecies even though the factors that regulate speciation rates at macroevolutionary scales are presumably not coupled to the rates of evolution of reproductive isolation (Rabosky and Matute 2013).

For the particular case of the radiation of *Setophaga*, these results question the importance of ecological opportunity as a limiting factor in the diversification of the clade. Instead, the lower, yet constant, rate of diversification during the latest part of the radiation might reflect other phenomena such as higher extinction or lower speciation rates due to the

cyclical glaciations of the Pleistocene (Zink and Slowinski 1995). This would also be congruent with other hypothetical scenarios proposed for this clade, as well as other North American radiations suggesting the divergence of these forms in allopatry (Bermingham et al. 1992; Johnson and Cicero 2004; Mengel 1964; Milá et al. 2000; Milá et al. 2007; Weir and Schluter 2004; Zink and Klicka 2006; Zink et al. 2004), which would not depend on ecological competition with another species in the clade. Additionally, current geographic distributions and ecological interactions of these species might solely be a result of their expansion after the last glacial maximum (Jablonski 2008). Thus, a detailed biogeographic study framed in absolute time and taking into account the distribution dynamics during the glacial cycles is required to truly understand the processes behind the diversification of this clade.

More generally, the ubiquity of diversity-dependent diversification, and its attribution to ecologically-mediated limits have been questioned by multiple authors (Cracraft 2010; Moen and Morlon 2014; Ricklefs and Jønsson 2014). My results suggest that taxonomic delimitation cannot be ruled out as the cause of patterns reported by multiple studies finding an asymptotic accumulation of lineages through time (reviewed by Rabosky 2013). Moreover, whereas some studies of radiations like tanagers, which are based on biospecies (Burns et al. 2014) show a slowdown in

diversification rates, other studies, including dipsadine snakes (Burbrink et al. 2012), all bird species (Jetz et al. 2012), and ovenbirds (Derryberry et al. 2011) find a constant accumulation of lineages through time, even when the latter shows patterns of morphological evolution consistent with an adaptive radiation. Importantly, however, these latter two studies are based on biospecies, and the patterns depicted in them are likely to become increasingly exponential as more taxonomic diversity is included.

1.5. FIGURES

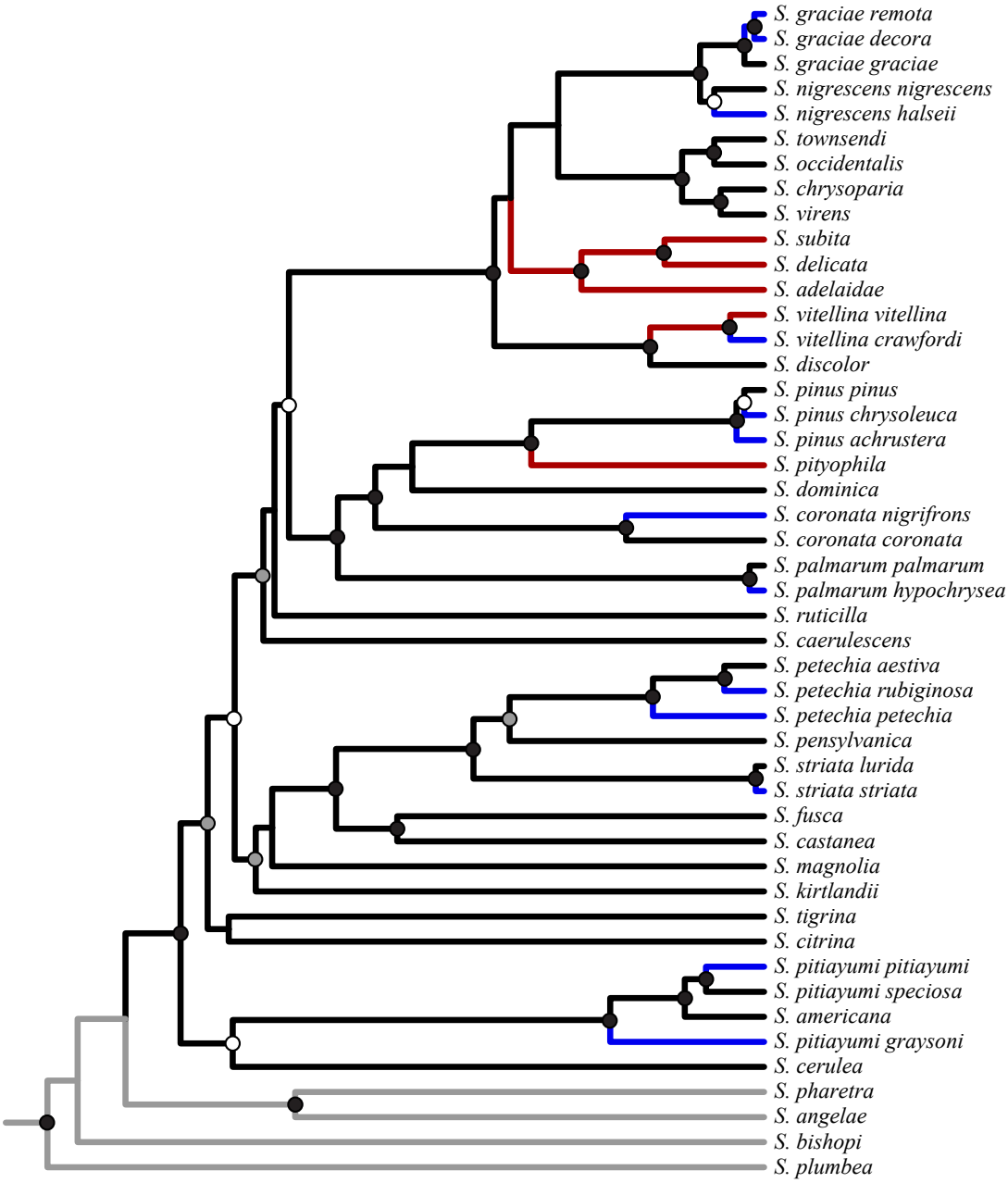

Figure 1.1. Ultrametric MCC trees from BEAST analyses of the three sets of taxa of the genus *Setophaga* analyzed in this paper: (Black) 25 taxa of

only North American biospecies (Rabosky and Lovette 2008a), (red) 30 taxa including all biospecies of the clade and (blue) 43 taxa including delimited phylospecies. Circles on nodes represent support values (posterior probability): white are values greater than 0.85, grey greater than 0.95 and black represent a posterior probability of 1.

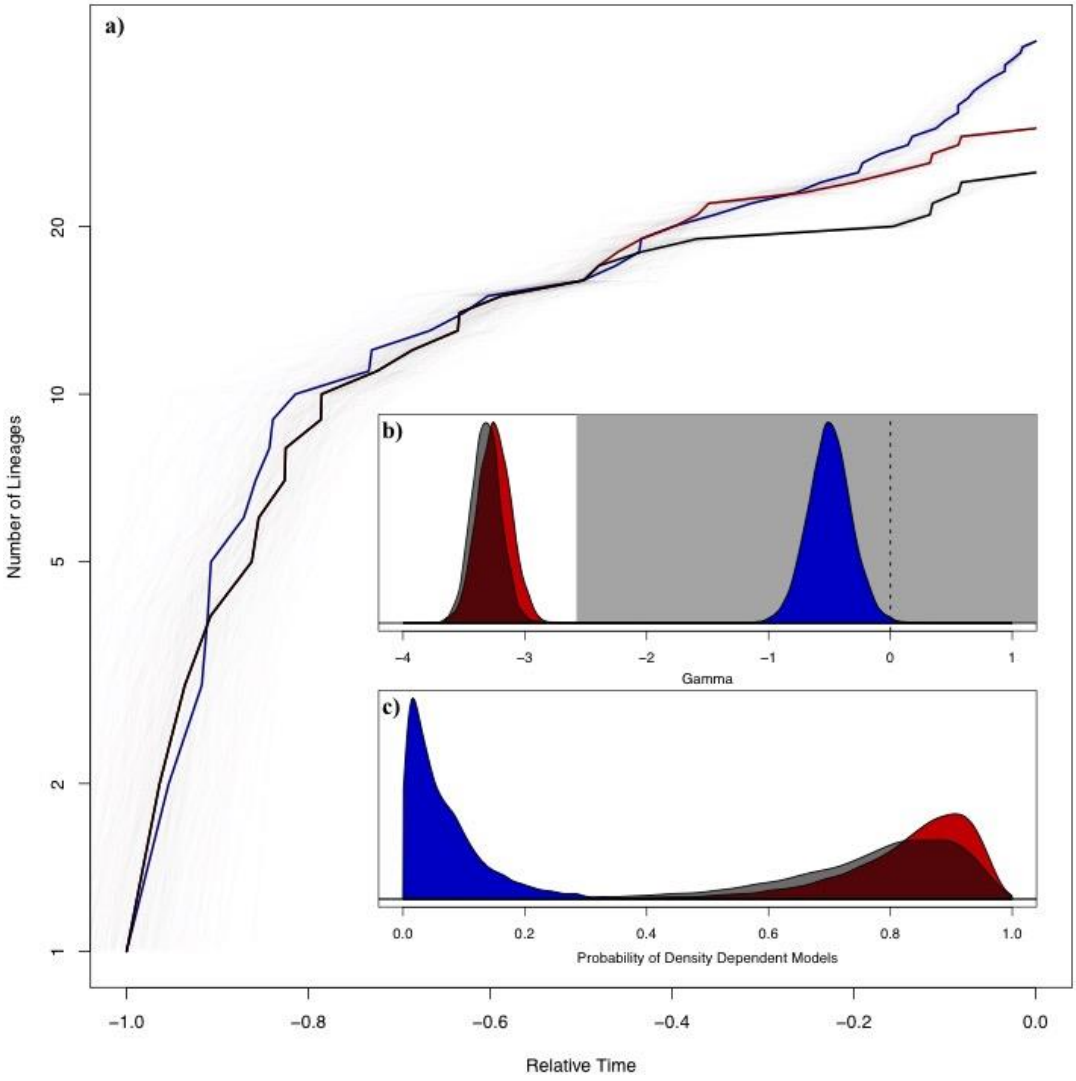

Figure 1.2. Diversification rates analyses based on the resulting distribution of trees of the BEAST analyses for wood-warblers of the genus *Setophaga*: (A) Lineage through time (LTT) plots of 200 randomly selected trees (thin lines), and the MCC tree (thick line). (B) Distribution of the gamma statistic across the sets of taxa examined. Negative gammas indicate a slowdown in diversification rates, and values outside the grey area are significantly ($p < 0.01$) different from 0. (C) Distribution of the

probability of diversity-dependent models being the best fit to resulting set of trees of the BEAST analyses calculated from the AIC of the likelihood based diversification rate analyses. Colors represent the three sets of terminal taxa: (black) North American biospecies, (red) all biospecies and (blue) phylospecies.

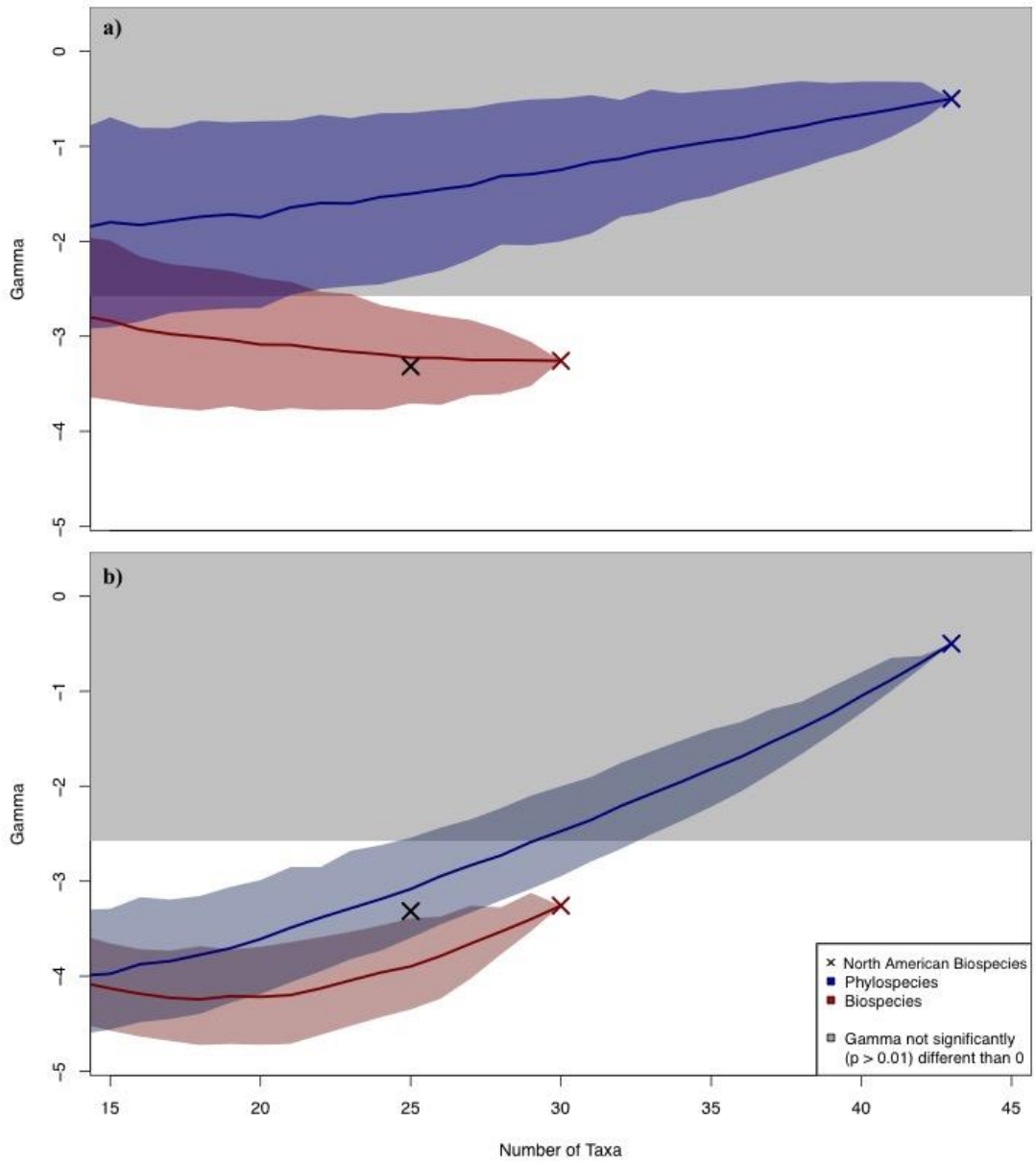

Figure 1.3. Distribution of gamma statistic values (y-axis) based on 500 iterations of trimmed trees with an incomplete number of terminal taxa (x-axis), for wood-warblers of the genus *Setophaga*. Trees were derived from the MCC trees of (red) all biospecies and (blue) phylospecies. The

probability of not including a tip in each iteration was (A) the same for all taxa and (B) inversely proportional to the length of the terminal branch leading to it. Lines represent the mean across all iterations and shades represent the interval in which 90% of the values are found. The empirical values for each of the set of terminal taxa are marked with crosses. Negative gamma values indicate a slowdown in diversification rates, and values outside the grey area are significantly different from zero.

1.6. ANNEXES

Table 1.S1. Samples of wood-warblers of the genus *Setophaga* included in this study and their taxonomic assignment. Superscripts represent in which dataset they were included: N = North American biospecies, B = All biospecies, and P = Phylospecies.

Table 1.S2. GenBank accession numbers for ND2 and CytB for the samples of wood-warblers of the genus *Setophaga* used in this study. Bold accession numbers where sequenced for this study (Note: new samples are marked with "+", they will be available on GenBank after publication).

Table 1.S3. GenBank accession numbers for Rho1, Myo2, Musk4, Aco9 for the samples of wood-warblers of the genus *Setophaga* used in this study. Bold accession numbers where sequenced for this study (Note: new samples are marked with "+", they will be available on GenBank after publication).

Figure 1.S1. Maximum likelihood tree of all individuals of the genus *Setophaga* sampled for mtDNA. Note that all biospecies are monophyletic with the exception of the Tropical Parula (*Setophaga pitiayumi*).

Relationships in this tree are congruent with those in Rabosky and Lovette (2008a) and Lovette et al. (2010).

Figure 1.S2. Probability of diversity-dependent models (y-axis) being the best fit to 500 iterations of trimmed trees with an incomplete number of terminal taxa (x-axis), for wood-warblers of the genus *Setophaga*. Trees were derived from the MCC trees of (red) all biospecies and (blue) phylospecies. The probability of not including a tip in each iteration was (A) the same for all taxa and (B) inversely proportional to the length of the terminal branch leading to it. Lines represent the mean across all iterations; shades the interval in which 90% of the values are found. The empirical values for each of the set of terminal taxa (Figure 1.2b) are marked with crosses.

2. NICHE MODELS USING CLIMATE AND POLLEN PREDICTORS REVEAL ABIOTIC AND BIOTIC DRIVERS OF DISTRIBUTIONS IN NORTH AMERICAN WOOD-WARBLERS

2.1. INTRODUCTION

Understanding how biotic, abiotic and historical factors interact to shape species' distributions has been and remains a central question in ecology, evolution, and conservation biology (Gaston 2009; Sexton et al. 2009). The role of climatic factors, in particular, has dovetailed with the development of Species Distribution (SDM) or Ecological Niche (ENM) Modeling methods that aim to characterize the ecological space in which a species occurs and identify geographical areas of climatic suitability (Peterson et al. 2011). However, studies linking biotic factors to continental-scale distributional patterns remain scarce (reviewed in Araújo and Rozenfeld 2014; Wisz et al. 2013)

Climatic factors have been demonstrated to limit species distributions using both correlative (Lima et al. 2007) and physiological (Parker and Andrews 2007) studies. However, dispersal limitations not directly related to abiotic conditions are an additional key factor shaping species' geographical ranges. Specifically, at a given time a species might occupy

either all or a fraction of the geographical space in which conditions are favorable. For example, transplant experiments in monkeyflowers in western North America showed that these species occupy the entire altitudinal range in which they can grow within that geographic region (Angert and Schemske 2005). However, such cases of a species in “distributional equilibrium” (when it occupies all areas in a region with favorable conditions) are not the norm (Araújo and Pearson 2005). The extent of distributional "disequilibrium" (when a portion of a species' potential range is not occupied) depends on factors such as colonization history, dispersal capability, biogeographical barriers, biotic interactions or even human impacts (Araújo and Pearson 2005; Fløjgaard et al. 2011; Hara 2010; Peterson et al. 1999; Svenning et al. 2008).

Whereas modeling abiotic suitability (i.e. based on climatic variables) has received most of the attention from the ENM community, the extent to which biotic interactions affect large-scale distributional patterns has typically been disregarded (Pearson and Dawson 2003; Peterson et al. 2011). Nevertheless, several studies have linked biotic interactions to range limits (reviewd in Louthan et al. 2015; Wisz et al. 2013), and simulation analyses suggest that patterns resulting from positive biotic interactions (i.e. mutualism and commensalism) manifest across all scales (Araújo and Rozenfeld 2014). As called for recently, integration of biotic

interactors into ENMs represents a key necessary advance, especially given the pressing need to forecast the effects of anthropogenic climate change on species distributions (Anderson 2013 and references therein; Blois et al. 2013b).

The BAM framework of “Biotic, Abiotic, and Movement” factors (Fig.2.1 ; Peterson et al. 2011; Soberón and Peterson 2005) formally describes the regions in which a species is distributed as the intersection of areas that meet certain ecological and historical requirements. In it, the area of a continent is depicted as a Venn diagram (Fig. 1) in which a geographical region (G) is divided into three overlapping sets: first, (A) areas with abiotic conditions in which the species can subsist; second, (B) areas in which the biotic composition includes interacting species that are necessary for the focal species and excludes prohibitive ones; third, (M) areas where the species is not limited by geographic barriers to movement (i.e., dispersal; note later extensions to demographically related restrictions in small areas of suitable conditions; Anderson 2013). Different configurations of the BAM diagram are commonly used to illustrate, from a theoretical point of view, how each of these classes of factors (abiotic, biotic, and movement) limits distributions of species (e.g. Fig. 3.5 in Peterson et al. 2011). However, despite a recent surge in studies investigating the role of biotic interactors in determining species ranges by

including biotic variables as additional predictor variables (Anderson in press), an empirical approach to model and map the areas that are suitable for a species based on abiotic, biotic, and movement factors remains lacking. Furthermore, previous studies addressing biotic interactions, and their effect on species distributions, have been limited to testing whether including biotic predictors improves the performance of correlative climate-based ENMs.

Here, I aim to disentangle the effect of abiotic, biotic and movement factors as determinants of the geographical distributions of a group of North American Wood Warblers (Parulidae). For six species of the genus *Oreothlypis*, I modeled the necessary abiotic and biotic conditions and identified the suitable geographic areas in North America by including predictor variables that fall into these categories (climatic conditions and palynological data, respectively) and taking current dispersal barriers into account. Importantly, wood-warblers show a strong association with the forest types in which they occur, particularly during the breeding season (Curson 2010; Curson et al. 1994), indicating that the availability of a particular floristic composition (e.g., that which can be characterized with palynological data) can limit their distributions. Here, the quantification of environmentally-suitable areas is not intended to characterize the complete set of abiotic or biotic factors limiting these species' distributions,

and interactions with other organisms (such as competition, predation or parasitism) would not be captured by climatic or palynological data. Furthermore, it is reasonable to assume that vegetational composition is not affected by the presence of the wood-warblers themselves and thus can be used as a predictor in correlative ENMs (i.e., the pollen data represent scenopoetic factors *sensu* Soberón (2007; Anderson in press). Additionally, because the bird-plant interaction is assumed to be positive-neutral (analogous to commensalism) it can be expected to manifest in a species' geographical range at regional and continental scales (Araújo and Rozenfeld 2014).

ENMs based on these two independent sources of environmental information, along with explicit consideration of regions accessible to each species (without internal barriers to dispersal) allow for tests of abiotic and biotic limits to the distributions of the various focal species in North America. Specifically, the following three scenarios exist for ENMs generated within a geographical region delimited to reflect areas without internal dispersal barriers: (1) if a species' distribution is limited by climatic factors, biotically suitable areas should exist outside the range of the species, with the species occurring only in the more restricted, climatically-suitable areas (Fig. 2.2A). Conversely, (2) if biotic factors (i.e. vegetation composition) are limiting, some areas outside the distribution would be

climatically suitable and the species would occur only in a smaller set of biotically suitable areas (Fig. 2.2B). Alternatively, (3) if abiotically and biotically suitable areas are congruent, it would not be possible to disentangle their relative importance to the limits of a species' distribution. In this latter case, the species would occupy all suitable areas (i.e. distributional equilibrium; Fig. 2.2C). However, if dispersal restrictions or other factors not captured by the climatic or pollen datasets are limiting, the species would not be present in all suitable areas of the continent, but rather only those within the region lacking internal barriers to dispersal (Fig. 2.2D). The latter two scenarios (Fig, 2.2C and D) represent cases in which climate and pollen-based ENMs would have similar predictions. However, incongruence is expected in the former two scenarios (Fig. 2.2A and B) in those cases, the areas predicted by the models made based on the limiting variables (climate or pollen, respectively) would be most similar to ENMs built using both sets of variables together.

2.2. METHODS

2.2.1. Focal Species

We obtained records for six of the seven North American species of *Oreothlypis* wood warblers (Lovette et al. 2010): the Orange-crowned Warbler (*O. celata*), Virginia's Warbler (*O. virginae*), the Tennessee Warbler, (*O. peregrina*), Lucy's Warbler (*O. luciae*), the Nashville Warbler (*O. ruficapilla*) and the Calaveras Warbler (*O. ridgwayi*). The geographical ranges of these species cover almost all forest types in North America, varying from broadly distributed species such as the Orange-crowned Warbler (*Oreothlypis celata*), to narrow montane habitats as in Virginia's Warbler (*O. virginiae*). Although the Nashville and Calaveras Warbler have traditionally been considered conspecific, molecular data indicate they are not each other's closest relatives in the group (Chapter 3 in this dissertation). Additionally, because of the paucity of locality and palynological data for the Colima Warbler (*O. crissalis*), it was not included in the study.

2.2.2. Environmental Variables

I used two different sources of variables to describe the environmental niche of each species. First, the abiotic factors were based on climatic data from WorldClim (Hijmans et al. 2005) that were interpolated from monthly data from meteorological stations across the globe. The complete WorldClim dataset includes 19 bioclimatic variables; eight that describe the average, extremes and variability of temperature and precipitation were employed in this study (Table 2.1).

The second source of variables, related to the biotic-scenopoetic requirements (see above) of each species, was derived from palynological data (Late Quaternary North American Vegetation Dynamics Data; Williams et al. 2004) in which the relative abundances of 55 taxa were sampled from lake-deposit pollen and interpolated on a geographic grid. Pollen data from Williams et al. (2004) were identified to various taxonomic levels; therefore they required further classification into 15 derived variables in which pollen percentages of each taxa were pooled together as plant functional groups (Table 2.1 and 2.S1; based on Williams et al. 1998). A key assumption is that palynological data at this resolution reflect the vegetation structure in the proximity of the lakes in which the pollen was deposited (Sugita 2007) and that the pollen-vegetation relationship is the same across the continent. It is worth noting that more complex pollen-vegetation models (PVMs; e.g. Dawson et al.

2016, and references therein) have been developed, but their application has been at more localized areas than the continental scale.

Both datasets were projected from their original format into a longitude-latitude WGS84 projection with a 0.5º resolution and an extent covering North America using the raster (Hijmans 2015) and rgdal (Bivand et al. 2015) packages in R 3.1.3 (R Core Team 2014). Because data from pollen deposits were sparse, and to avoid over-interpolation, not all cells in North America were included in the original generation of the pollen data (Williams et al. 2004). Therefore, areas in which climatic data were present but pollen data were lacking were not used in this study.

2.2.3. Locality Data

Presence records for each of the species were obtained from the E-bird database (Sullivan et al. 2009). The total number of records for each species ranged from ~18,000 to 415,000. I restricted analyses to the portion of records that were observed during two months of the breeding season (June 15th to August 15th) and that were within 100 km of the accepted breeding distribution of each respective species (available at natureserve.org; Ridgely et al. 2007). The total unique localities ranged from ~2,300 to 22,000 per species. Because of the coarse resolution of

the environmental data and substantial aggregation of records around highly-sampled areas, only one locality per cell was used, for a total of 84 to 1087 unique cells recorded per species.

2.2.4. Study Region

Ecological niche models are built on the assumption that environmental variables used to model the niche (or others correlated with them) are the only factors limiting the geographical distribution within the training area (Peterson et al. 2011). To meet this expectation (see Noise Assumptions of Anderson 2013), the region from which environmental data are drawn should be restricted to areas in which there are no biogeographical restrictions to the presence of the species, (i.e., within which no dispersal barriers exist; M in Fig. 2.1). Additionally, the study region should not include areas where unexamined biotic factors limit the species' distribution (B in Fig. 1; Anderson and Raza 2010). In these parapatrically distributed wood-warblers, competitive interactions likely restrict the distributions of some species that come into geographic contact (Krosby and Rohwer 2010).

In order to build distribution models that fit these assumptions, I defined species-specific training areas (orange area highlighted on Figure 2.3A)

through a two-step process. First, I excluded regions to which the species likely has not had the opportunity to disperse by defining an area including the known breeding distribution of each species based on NatureServe's breeding range (Ridgely et al. 2007) with a 500 km buffer around it. Second, I took into account the possible effect of inter-specific competition by excluding areas in which other non-sympatric species of this group occur. The resulting study regions for each species are areas in which the species can be expected to be in environmental equilibrium with respect to the variables used in the models.

Because the E-bird presence locality data were highly biased (i.e. grid cells in more accessible areas and closer to urban centers that have been more heavily sampled), I corrected for the potential effect of geographical sampling differences on ENMs. To do so, background data used to train the model should be proportional to the sampling effort that led to the presence locality data (Phillips et al. 2009). To produce such a dataset, I first created a sampling-effort raster in which the value of each cell was the number of times it had been sampled based on the entire eBird dataset for the same dates as the occurrence data. Background data were then selected by sampling without replacement 70% of the cells within the background area defined for each species, where the probability of a cell being sampled was proportional to the number of sampling events

(weighted target group approach of Anderson 2003). There are two reasons for sampling background data without replacement here. First, only one locality record per cell was used in the presence dataset. Second, if the probability of sampling *with* replacement had been proportional to the sampling effort, a computationally-unfeasible amount of background points would be required to capture a representative portion of the ecological space (because the number of sampling events in some cells was orders of magnitude larger than in others).

2.2.5. Model Selection and Projection

Ecological Niche Models were made in MAXENT, version 3.3.3.k (Phillips et al. 2006) using the dismo (Hijmans et al. 2016) package in R 3.13. To select key species-specific settings related to model complexity for Maxent, I used the ENMeval R package (Muscarella et al. 2014), to build and evaluate multiple candidate models with various combinations of the regularization multiplier and feature classes allowed (see below). I used the block partitioning method of ENMeval, in which the study area was partitioned into four spatial bins (different colors for localities in Fig. 2.3A), three of which were used to train the model in each iteration while the remaining one was withheld for evaluation.

Niche models were built with three sets of variables: (1) climate only, (2) pollen only, and (3) climate-and-pollen. For each of the three sets of variables, 180 total models were made per species. These models were built using 60 different combinations of settings in which the complexity of the feature classes included and regularization multiplier varied. We used ENMeval's default feature classes combination and the regularization multiplier varied from 1 to 5 in intervals of 0.5 units. The best model was selected under two sequential conditions: information criteria and transferability. First, to select the best-performing settings, only the candidate models within two units of the lowest AICc score (Warren et al. 2008) were considered. Second, when more than one model had a delta-AICc lower than two, the one with the lowest difference between training and testing AUC was selected to maximize geographic transferability (Radosavljevic and Anderson 2014; Warren and Seifert 2011). The settings selected for each species (for each environmental dataset) were then used to build ENMs using the unpartitioned presence and background data. For each species, the ENMs based on each of the three sets of variables were projected onto the entire continent, therefore estimating all environmentally suitable areas in North America, regardless of whether or not the species actually occurs in those areas or not. Projections into non-analog environments (conditions present in North America, but not within the training area of a particular species) were

made by allowing Maxent to extrapolate responses beyond the range of the variables in an unconstrained manner (i.e. not “clamping”; Elith et al. 2011). To examine the individual contribution of each variable, response curves of ENMs were examined using MAXENT’s explain tool (Phillips et al. 2006).

2.2.6. Distance Matrix and Multidimensional Scaling

To examine the overall congruence of the various species’ ENMs, I computed a distance matrix among all resulting projections. Suitability maps of all species based on each of the three sets of variables were compared pairwise among species. The distance between two raster grids was equal to 1 - Schoener’s *D* (Schoener 1968; Warren et al. 2008) calculated using the nicheOverlap function in dismo (Hijmans et al. 2016). The value of the comparison of two maps ranges between 0 and 1, with identical maps having a value of 0 and very dissimilar maps having a value close to 1. To visualize these distances in a two-dimensional space, I then performed a Nonmetric Multidimensional Scaling (MDS) analysis using the vegan (Oksanen et al. 2016) package in R.

2.2.7. Empirical BAM Diagrams

I tested the predictions outlined in the Introduction by examining results via empirical BAM quantifications and visualizations. To compute BAM diagrams for each species, I first defined the total biotically- and abiotically-suitable regions by applying a 10% training omission-rate threshold to the continental projections of the climate-only and pollen-only models (A and B sets in BAM, respectively; Pearson 2004; Peterson et al. 2011). As mentioned earlier, I approximated the “movement” (M set) of BAM as the species-specific area from which the background data were drawn for each species. I subsequently calculated the total area deemed suitable by both climate and pollen (via the separate models) as well as their overlap using the raster package in R. The Euler diagrams depicting the relationships among the “Biotic, Abiotic, Movement” areas were first calculated in R and then illustrated using the Venn Charts tool in Google Chart’s API (http://developers.google.com/chart/).

2.3. RESULTS

The final maps of environmental suitability based on models built with three different sets of variables (climate only, pollen only, and pollen-and climate) for each species indicated various patterns of geographic concordance. For example, the projection of suitable conditions in North America for the Tennessee warbler for the three sets of environmental data differ: climate only (Fig. 2.3B), pollen only (Fig. 2.3C) and climate-and-pollen (Fig. 2.3D; corresponding figures for all other species can be found in supplementary figures 2.1-2.5). As expected, models built with climate and pollen together predicted a more restricted distribution of suitability than did models built with either pollen or climate independently.

The extent to which abiotically- and biotically-suitable areas overlapped when projected to the full extent of North America varied greatly across taxa. Congruent with the predictions of correspondence between biotic and abiotic factors (Fig. 2.2C-D), the respective climate-only and pollen-only models were virtually identical in the Orange-crowned, Nashville, Tennessee, and Lucy's warblers (Fig. 2.4). However, climate-only and pollen-only models were conspicuously different from each other, and from the pollen-and-climate models for Virginia's and Calaveras warblers (orange and yellow symbols on Fig. 2.4, respectively). Notably, two

opposing patterns were recovered regarding their distance to the climate-and-pollen models. On the one hand, the pollen-only model for the Virginia's warbler was closer to its climate-and-pollen model, congruent with the prediction of biotic limits to its distribution (Fig. 2.2B). On the other hand, for the Calavera's warbler, consistent with limiting climatic factors (Fig. 2.2A), the climate-only model was more similar to the one based on both climate-and-pollen than was the pollen-only model.

The patterns above were upheld by the BAM diagrams constructed for each species based on ENMs (Fig. 2.5). Suitable areas predicted by pollen and climate variables independently overlapped broadly for the Orange-crowned, Nashville, Tennessee, and Lucy's warblers (Fig. 2.5A, B, C, E). For those species, when ENMs were projected to North America, areas abiotically and biotically suitable outside the training area (M) of the species were scarce. This is consistent with the scenario of distributional equilibrium (Fig. 2.2C), in which the most important factor limiting the species' distribution in the continent is included in the ENMs, and the species occupy all suitable areas available.

In contrast, areas from which Virginia's Warbler (Fig. 2.S5) is absent in eastern USA were predicted to be climatically suitable. Concordant with the scenario of biotic limitations (Fig. 2.2B), suitable areas based on pollen

data were largely restricted to vicinity of presence records for this species (Fig. 2.5F). Concretely, high relative abundance of two plant functional groups related to mixed and deciduous forest account for the low suitability in the east. Reflecting the difference in forest composition among these areas, Virginia's Warbler required a large representation (over 40% of relative pollen abundance) of the "eurythermic conifer" functional group species (such as junipers of the Cupressaceae family; Table 2.S1). In contrast, areas in which either "temperate summer-green" or "warm temperate evergreen" represented over 15% of the relative pollen abundance were estimated as not suitable.

In contrast, and consistent with abiotic limits to distributions (Fig. 2.2A), the Calaveras warbler's climate-based ENM predicted a more restricted area than the one based on pollen, which indicated suitability in southwestern Canada where the species is absent (Fig. 2.5D). These biotically suitable areas experience unsuitably-low temperatures, and higher temperature seasonality than the modeled tolerances of the Calaveras Warbler (response curves not shown).

Importantly, cases like the Tennessee Warbler (which does not occur in western Alaska) for which biotic factors seemed to be limiting (Fig. 2.3 and 2.5C), suggest that this species did not perfectly match only one of the

hypothetical scenarios in Figure 2.2 across all of its distribution. For this species, the abundance of boreal conifers was the variable that contributed the most to the model (as determined by this variable having the largest lambda weight in the ENM). Specifically, only areas in which pollen of species classified as “boreal conifers” accounted for more than 20% of the palynological composition were considered as suitable for the Tennessee Warbler. Low suitability in western Alaska is explained by the change of a community dominated by boreal conifers into one with a large representation of “cool temperature summer green” plants west and north of the northern Rocky Mountains.

2.4. DISCUSSION

As possible limits to species distributions, abiotic and biotic factors have often been treated as alternatives (e.g. Cumming 2002), but the current results indicate the utility of comparing models based on them separately and together. The fact that pollen-only and climate-only models broadly overlapped for most of the taxa examined confirms that abiotic and biotic factors are not geographically independent of each other for these species. Furthermore, for four species – Virginia’s, Orange-crowned, Tennessee, and Nashville warblers – most biotically suitable areas are also climatically suitable (and vice versa), which suggests that the plant

communities in which these species occur are strongly affected by climate. It is worth noting that using climate and pollen data simultaneously produced the closest predictions to the actual geographical range for models when projected to the entire continent, but with only slight improvements over models made with one or the other (depending on the species involved, diamonds in Fig. 2.5). Additionally, with the exception of the Calaveras Warbler, all species occurred across most of the abiotically and biotically suitable areas available on the continent, which suggests distributional equilibrium in North America. This pattern was also supported by the empirical BAM diagrams (Fig. 2.5), in which nearly no abiotically- and biotically-suitable areas (the intersection of A and B in Fig. 2.4) were outside the available areas for each species (M).

At odds with the view that abiotic factors constitute the primarily limitations for species' distributions at a continental scale (Pearson and Dawson 2003), only one of the six taxa examined (the Calaveras warbler) exhibited a pattern consistent with solely climatic limitation, specifically low minimum temperatures and high temperature seasonality (Fig 2.2A). Importantly, however, the role of climatic factors shaping a species' geographical range cannot be discounted in those species for which independent models based on either climate or pollen had similar predictions. Moreover, climatic factors could play an indirect role through other biotic factors not

explicitly examined here. For example, the availability of prey species (Price and Gross 2000), host species (Bozick and Real 2015; Gutierrez et al. 2005), or the lack of competition (Gutierrez et al. 2014; Taniguchi and Nakano 2000) or disease (Lips et al. 2008) could ultimately depend on the climatic limitations of the interacting species. In such a case, the effect of these interactions on a focal species' distribution would also be captured by the climatic variables used (Anderson 2013; Anderson in press).

Furthermore, biotic data alone clearly provided relevant information not accounted for in climate-only ENMs for at least two species. For the Virginia's warbler, and to a lesser extent the Tennessee warbler, climatic models predicted more regions outside a species' distribution to be suitable than did the pollen dataset. For the Virginia's warbler – a species specialized to pinyon-juniper woodlands (Curson 2010; Curson et al. 1994) – climatically-suitable areas in eastern North America, where this forest type does not occur, did not contain high enough abundances of the conifer species required by the Virginia's warbler. Similarly, the dominance of species in the functional group "cool temperature summer green" in northwestern Alaska was not suitable for the Tennessee Warbler, which during its breeding season is strongly associated with the spruce budworm (McMartin et al. 2002; Patten and Burger 1998) and is distributed in boreal-conifer dominated areas. The fact that pollen-based models

correctly predict the absence of suitability for the species in climatically-suitable areas suggests that these biotic factors (i.e. plant species) could have been affected similarly by historical events as the focal wood-warbler species. Historical processes such as post-glaciation range expansion, the inability to cross geographical barriers (i.e. the Rocky Mountains), or vicariant events would affect fauna and flora simultaneously (yet likely in idiosyncratic ways), but modern climate might not reflect these patterns.

This study provides a novel framework for understanding the drivers of species' range limits at a continental scale. By estimating BAM diagrams empirically, I evaluated the importance of abiotic and biotic limits to species' distributions, harnessing a framework that previously had only been used theoretically (the "Biotic, Abiotic, and Movement" paradigm). These results show that for most of the taxa examined, the relative importance of climate and pollen could not be teased apart. However, in one case, biotic variables limited the distribution in areas climatically suitable, and the opposite occurred for another species. These results highlight the importance of considering potential effects of biotic interactions on species ranges, in particular when ENMs are projected across time and space and used as tools for biogeographical analyses (Kozak et al. 2008) or policy-making regarding invasive species and climate change (Louthan et al. 2015; Sax et al. 2013).

2.5. TABLES

Table 2.1. Biotic and abiotic variables included as environmental predictors

Climatic Variables - (Abiotic factors)		**Pollen Variables (Biotic factors)**	
Bioclimatic Variable	**Variable Code**	**Functional Group**	**Abbreviation**
Annual Mean Temperature	BIO1	Boreal Conifer	BorCon
Temperature Seasonality	BIO4	Cool Temperate Conifer	CoolTempCon
Maximum Temperature of Warmest Month	BIO5	Eurythermic Conifer	EuryCon
Minimum Temperature of Coldest Month	BIO6	Boreal Summer Green	BorSumGre
Annual Precipitation	BIO12	Cool Temperate Summer Green	CoolTempSumGre
Precipitation of Wettest Month	BIO13	Temperate Summergreen	TempSumGre
Precipitation of Driest Month	BIO14	Warm Temperate Summer Green	WarmTempSumGre
Precipitation Seasonality	BIO15	Warm Temperate Evergreen	WarmTempEvGreen
		Shrubs	Shrubs
		Sedge	Sedge
		Forbs	Forbs
		Grass	Grass
		Holly and Ericaceae	AqEric
		Legumes	Legumes
		Selaginella	Selagi

2.6. FIGURES

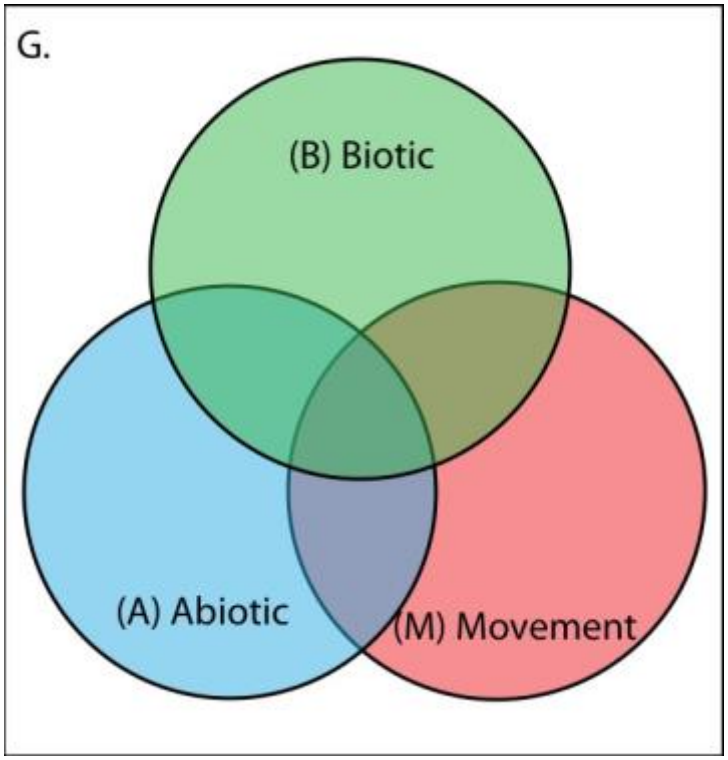

Figure 2.1. Modified from Soberón and Peterson (2005). “Biotic-abiotic-movement” (BAM) diagram representing the geographical areas where certain historical and ecological conditions required by the species are met. The blue area (A) represents the regions in which the abiotic conditions are suitable for the species. The green area (B) represents the regions in which a suitable combination of interacting species occurs. M (red) indicates the regions that have been available for a species (e.g., no barriers to dispersal). G represents the total geographical area of the study region.

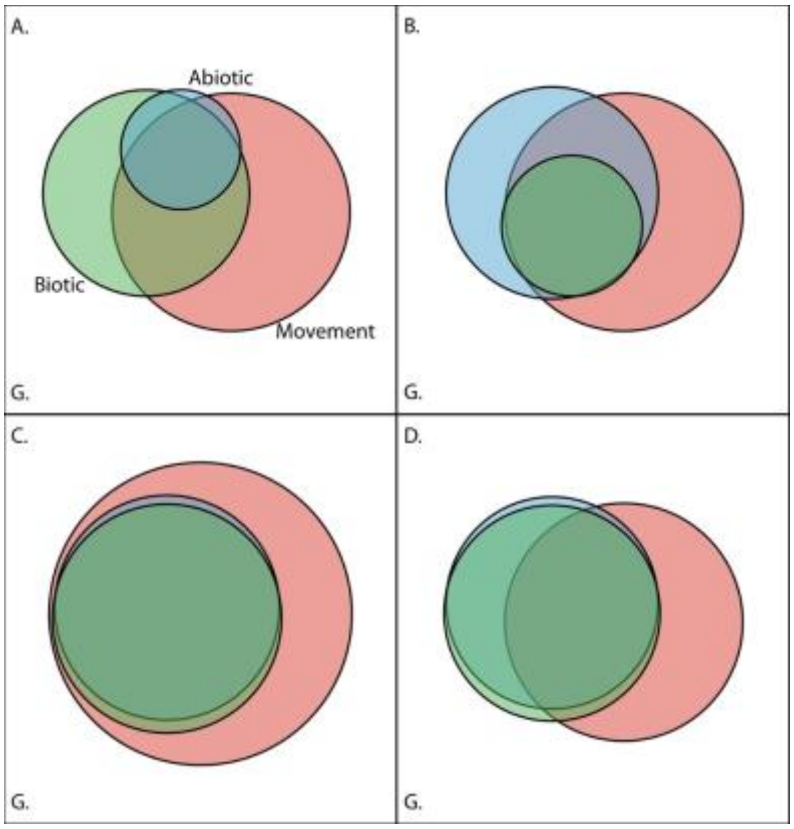

Figure 2.2. Hypothetical scenarios under which abiotic and biotic factors may limit species distributions represented by different configurations of the BAM diagram: (A) Predicted configuration if a species' distribution is limited by climatic factors. (B) Predicted configuration if biotic factors are limiting. The lower panels represent configurations in which biotically and abiotically suitable areas are congruent. (C) Predicted distribution if both of these factors limit the species' distribution. (D) Predicted configuration if "movement" restrictions or other factors not captured by the biotic or abiotic variables are limiting, beyond the confounded effects of abiotic and biotic factors.

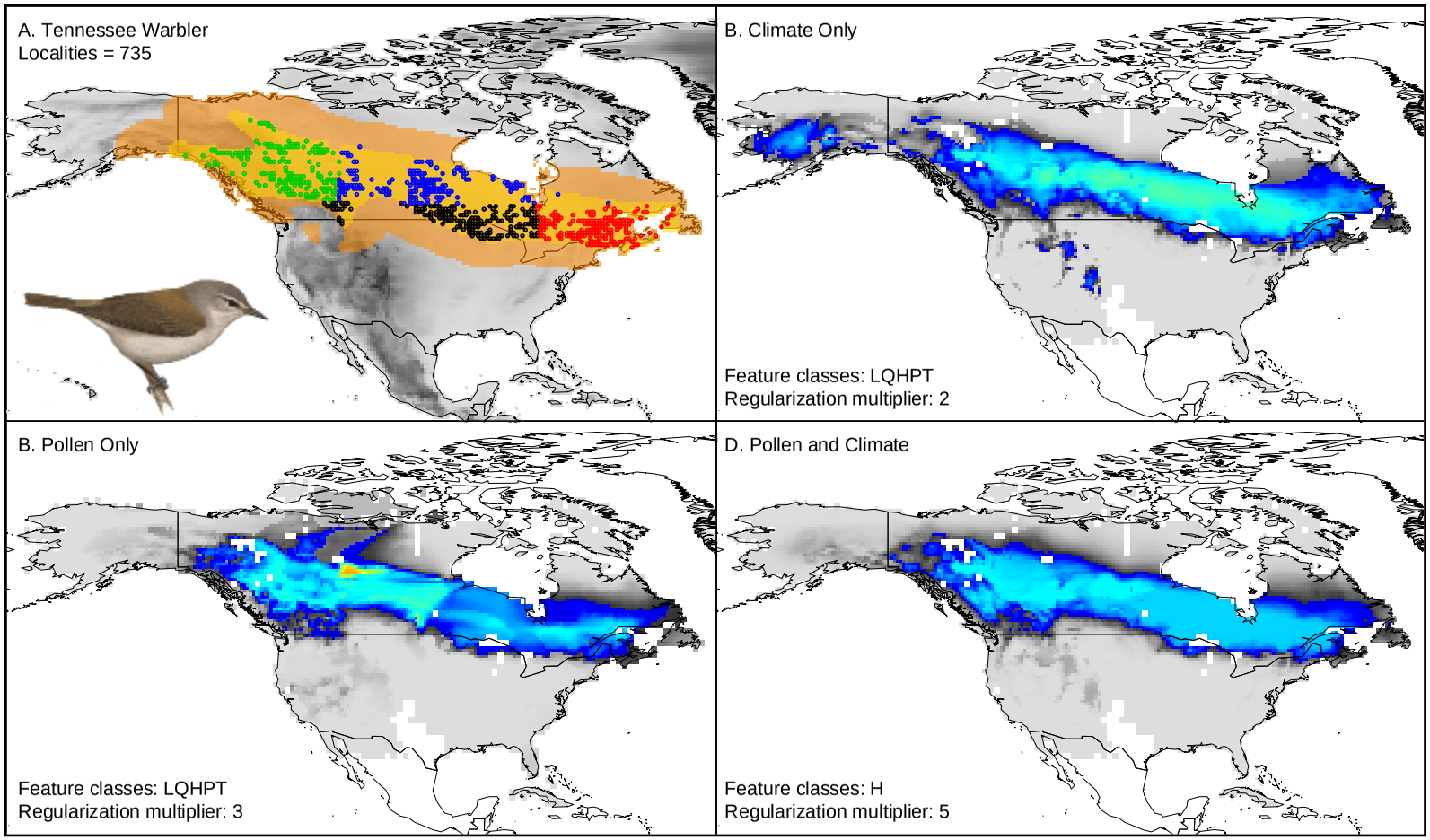
A. Tennessee Warbler
Localities = 735
B. Climate Only
Feature classes: LQHPT
Regularization multiplier: 2
B. Pollen Only
Feature classes: LQHPT
Regularization multiplier: 3
D. Pollen and Climate
Feature classes: H
Regularization multiplier: 5

Figure 2.3. Input data and Maxent ENM projections to all of North America for the Tennessee warbler. (A) Unique localities sampled (points), with colors representing the “block” partition in ENMeval (Muscarella et al. 2014); the solid polygon represents the breeding distribution of the species (Ridgely et al. 2007), and the semitransparent buffer indicates the areas from which the background data were drawn (M in Fig. 2.5D). Abiotically suitable areas predicted by ENMs based on climate-only variables (A in Fig. 2.5D); (C) Biotically suitable areas predicted by ENMs based on pollen-only variables (B in Fig. 2.5D); (D) Areas predicted to be suitable with ENMs based on both climatic and pollen data. For panels B-D, light to dark grays represent relative suitability below the respective 10% omission rate thresholds, and cold to warm colors show increasing suitability above those thresholds. Letters for feature classes stand for: L = Linear, Q = Quadratic, H = Hinge, P = Product, and T = Threshold. Similar figures for all other species appear in the Annexed Material (Figures 2.S1-2.S5).

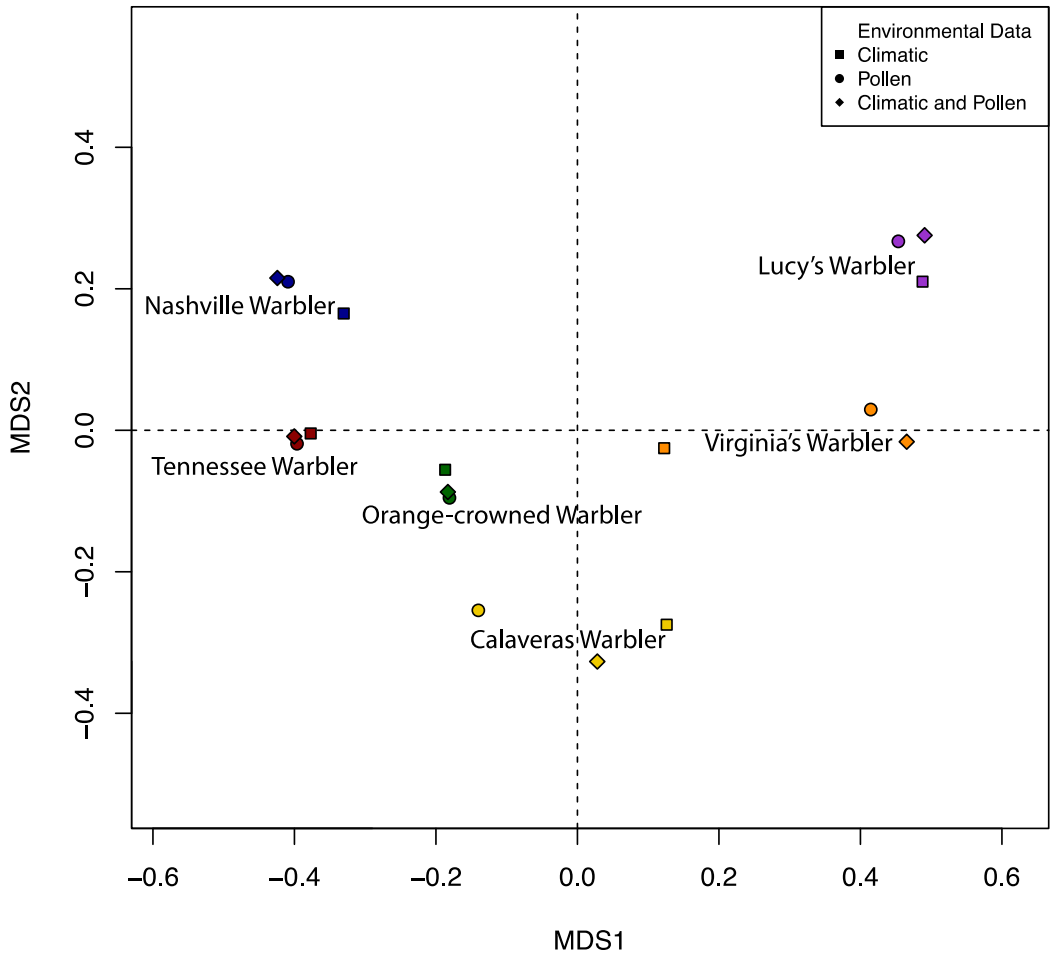

Figure 2.4. Multidimensional scaling (MDS) plot showing the relationship among the projected suitable areas for all species of warblers examined in this study. This plot visualizes the overall distances (1- Shoener's *D*) between (squares) climate-only ENMs; (circles) pollen-only ENMs and (diamonds) climate-and-pollen ENMs for each species (different colors).

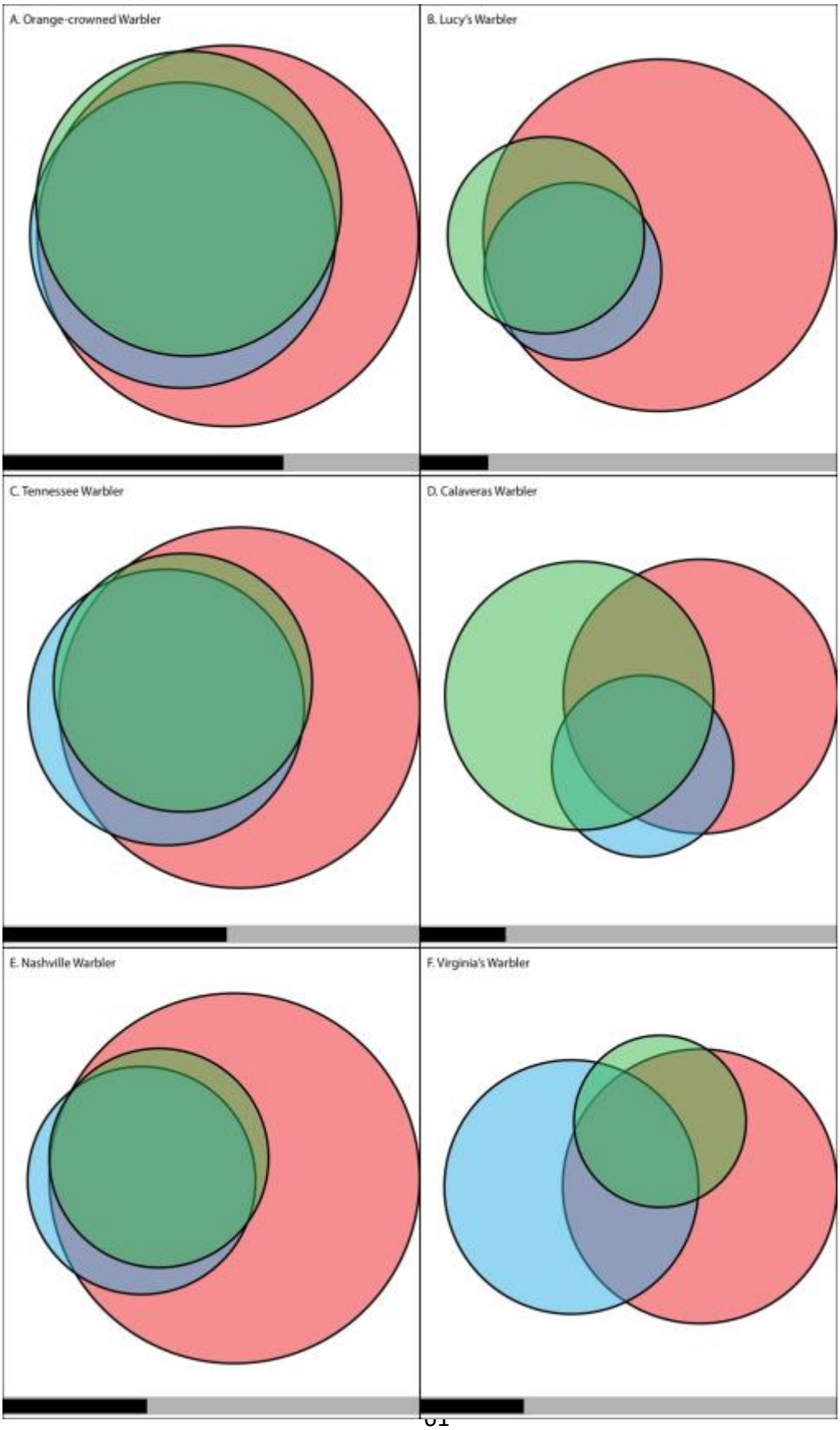
A. Orange-crowned Warbler
B. Lucy's Warbler
C. Tennessee Warbler
D. Calaveras Warbler
E. Nashville Warbler
F. Virginia's Warbler

Figure 2.5 Empirical “BAM” diagrams calculated for each species of warbler examined in this study. Blue areas represent *Abiotically* suitable regions based on climate-only ENMs. Green areas represent *Biotically*-suitable regions based on pollen-only ENMs. Red areas represent available areas within which *Movement*-related factors are not expected to be limiting (see text). The length of the black bar at the bottom of each diagram is proportional to the total area of the union of A, B and M, indicating the “zoom” for each species relative to the whole of North America (the sum of the black bar and the gray bar).

2.7. ANNEXES

Table 2.S1. Assignment of pollen taxa from Williams et al. (2004; rows) to plant functional groups (columns) modified from Williams et al. (1998). Abbreviations follow Table 1 in main text for functional groups and Table 2.S2 for pollen taxa.

Table 2.S2. Abbreviations of the 56 pollen taxa assigned to plant functional groups.

Figure 2.S1. Input data and ENM projections for the Orange-crowned warbler. (A) Unique localities sampled (points), with colors representing the "block" partition in ENMeval (Muscarella et al. 2014); the solid polygon represents the breeding distribution of the species (Ridgely et al. 2007), and the semitransparent buffer indicates the areas from which the background data were drawn (M in Fig. 2.5D). Abiotically suitable areas predicted by ENMs based on climate-only variables (A in Fig. 2.5D); (C) Biotically suitable areas predicted by ENMs based on pollen-only variables (B in Fig. 2.5D); (D) Areas predicted to be suitable with ENMs based on both climatic and pollen data. For panels B-D, light to dark grays represent relative suitability below the respective 10% omission rate thresholds, and cold to warm colors show increasing suitability above those thresholds.

Letters for feature classes stand for: L = Linear, Q = Quadratic, H = Hinge, P = Product, and T = Threshold.

Figure 2.S2. Input data and ENM projections for Lucy's warbler. ((A) Unique localities sampled (points), with colors representing the "block" partition in ENMeval (Muscarella et al. 2014); the solid polygon represents the breeding distribution of the species (Ridgely et al. 2007), and the semitransparent buffer indicates the areas from which the background data were drawn (M in Fig. 2.5D). Abiotically suitable areas predicted by ENMs based on climate-only variables (A in Fig. 2.5D); (C) Biotically suitable areas predicted by ENMs based on pollen-only variables (B in Fig. 2.5D); (D) Areas predicted to be suitable with ENMs based on both climatic and pollen data. For panels B-D, light to dark grays represent relative suitability below the respective 10% omission rate thresholds, and cold to warm colors show increasing suitability above those thresholds. Letters for feature classes stand for: L = Linear, Q = Quadratic, H = Hinge, P = Product, and T = Threshold.

Figure 2.S3. Input data and ENM projections for the Calaveras warbler. (A) Unique grid-cells sampled (points), with colors representing the "block" partition in ENMeval (Muscarella et al. 2014); the solid polygon represents the breeding distribution of the species (Ridgely et al. 2007), and the

semitransparent buffer indicates the areas from which the background data were drawn (M in Fig. 2.5D). Abiotically suitable areas projected by ENMs based on climate-only variables (A in Fig. 2.5D); (C) Biotically suitable projected by ENMs based on pollen-only variables (B in Fig. 2.5D); (D) Areas projected to be suitable with ENMs based on both climatic and pollen data. For panels B-D, light to dark grays represent relative suitability below the respective 10% omission rate thresholds, and cold to warm colors show increasing suitability above those thresholds. Letters in feature classes stand for: L = Linear, Q = Quadratic, H = Hinge, P = Product, and T = Threshold.

Figure 2.S4. Input data and ENM projections for the Nashville warbler. (A) Unique localities sampled (points), with colors representing the “block” partition in ENMeval (Muscarella et al. 2014); the solid polygon represents the breeding distribution of the species (Ridgely et al. 2007), and the semitransparent buffer indicates the areas from which the background data were drawn (M in Fig. 2.5D). Abiotically suitable areas predicted by ENMs based on climate-only variables (A in Fig. 2.5D); (C) Biotically suitable areas predicted by ENMs based on pollen-only variables (B in Fig. 2.5D); (D) Areas predicted to be suitable with ENMs based on both climatic and pollen data. For panels B-D, light to dark grays represent relative suitability below the respective 10% omission rate thresholds, and

cold to warm colors show increasing suitability above those thresholds. Letters for feature classes stand for: L = Linear, Q = Quadratic, H = Hinge, P = Product, and T = Threshold.

Figure 2.S5. Input data and ENM projections for the Virginia's warbler. (A) Unique grid-cells sampled (points), with colors representing the "block" partition in ENMeval (Muscarella et al. 2014); the solid polygon represents the breeding distribution of the species (Ridgely et al. 2007), and the semitransparent buffer indicates the areas from which the background data were drawn (M in Fig. 2.5D). Abiotically suitable areas projected by ENMs based on climate-only variables (A in Fig. 2.5D); (C) Biotically suitable projected by ENMs based on pollen-only variables (B in Fig. 2.5D); (D) Areas projected to be suitable with ENMs based on both climatic and pollen data. For panels B-D, light to dark grays represent relative suitability below the respective 10% omission rate thresholds, and cold to warm colors show increasing suitability above those thresholds. Letter in feature classes stand for: L = Linear, Q = Quadratic, H = Hinge, P = Product, and T = Threshold.

3. SPECIATION IN *OREOTHLYPIS* WARBLERS: INTEGRATING CLIMATIC MODELS, PALYNOLOGY AND BIOGEOGRAPHY

3.1. INTRODUCTION

The role of Earth-history in the origin and assembly of biodiversity is a central question in evolutionary biology. A significant geological event was the glacial cycles of the Pleistocene, which induced severe climate change globally including ice sheets covering a large portion of the Northern Hemisphere (Ehlers and Gibbard 2004). Evidence from pollen deposits (Davis and Shaw 2001), ecological niche modeling (ENMs;Martínez-Meyer et al. 2004; Waltari et al. 2007), and phylogeographical studies (Shafer et al. 2010; Soltis et al. 2006) have established that the ranges of most species shifted to the south during glaciations. Because of these climatic fluctuations, the geographical distributions of species have expanded and contracted in a cyclical manner, with many tracking the climatic and ecological conditions that were appropriate for them (Hill et al. 2011; Holt 2009). During glacial maxima, suitable regions for some species often represented the species' greatest contraction in geographical range (refugia; Stewart et al. 2010).

Isolation in refugia has been hypothesized to be a major mechanism for speciation in the Plestocene (Avise and Walker 1998; Haffer 1969; Mayr 1963; Mengel 1964; Weir and Schluter 2004). As an exemplar system, Robert Mengel (1964) proposed a model in which the radiation of North American wood-warblers (Parulidae) could be explained speciation events caused by cyclic series of fragmentation, niche differentiation, and expansion of species' ranges. Although multiple authors have proposed that fragmentation and neutral population dynamics could alone provoke origin of new taxa (Avise and Walker 1998; Haffer 1969; Mayr 1963; Weir and Schluter 2004), Mengel's model (1964) not only aimed to explain diversification and biogeographical patterns of this group, but also the variety of broad-scale habitats that wood-warblers currently occupy in North America.

Specifically, Mengel (1964) hypothesized that during periods of ecological harshness, such as glacial maxima, populations of northern species would be displaced to the south, causing the contracted and isolated populations to adapt to novel forest types. He also posited that transcontinental ranges would first be divided by glacial advances into eastern and western forms, generally to the east and west of the Great Plains, and that highlands in the west would act as barriers between the coastal and interior forests that had shifted southwards. Moreover, ecological specializations acquired in

periods when forested North American biomes were fragmented and compacted would be maintained during the subsequent expansion. Species distributed longitudinally across the northern continental forests during interglacial times would then be subject to fragmentation again in the following contraction phase of the next glacial cycle. Mengel thus hypothesized that present-day biogeographical patterns represent the outcome of these repeated cycles of ecological expansion and contraction.

Even though the relationships and divergence times predicted by Mengel's particular case studies (1964) were examined and questioned by molecular data over two decades ago (Bermingham et al. 1992), his general model has the potential for substantial predictive power and thus deserves further examination. Molecular data across multiple boreal species-complexes suggest that the Pleistocene climatic changes were a major factor promoting speciation in this region (Galbreath et al. 2010; Hewitt 2000; Puckett et al. 2015; Weir and Schluter 2004). Moreover, Weir and Schluter (2004) highlight the issue that biogeographical studies examining patterns of speciation of polytypic reproductively-isolated species (biospecies), excluding slightly differentiated forms, likely underestimate the importance of recent diversification (Sanín and Cracraft 2016; Zink et al. 2004). In fact, a number of phylogeographical studies in

birds place the divergence of phylogroups in the Late Pleistocene (Barrowclough et al. 2004; Klicka et al. 2011; Manthey et al. 2011; Spellman et al. 2007; Zink et al. 2000), and the geographical arrangement of these taxa is potentially congruent with Mengel's proposed mechanism. Similarly, systems in which changing climates has have hypothesized to promote taxonomic and ecological diversity have recently been supported by studies integrating phylogenetic, physiological and environmental data (Damasceno et al. 2014 and references there in).

Incorporating quantitative environmental data into biogeographical studies has been a useful approach to understanding how differentiation in climatic preferences can be linked to speciation. For example, Kozak and Wiens (2010a) found that salamanders having a high diversification rate also had rapid climatic niche evolution. Alternatively, niche conservatism has also been suggested to have increased the rate of speciation (Kozak and Wiens 2006; Kozak and Wiens 2010b), as it is essential for initiating allopatry as a consequence of the origin of an ecological barrier (Wiens 2004a). In more detailed studies examining lower taxonomic scales, the origin of sister taxa has been linked to divergence in climatic preferences (e.g. Smith and Donoghue 2010), climate-driven range-shifts have been proposed as a mechanism for divergence in parapatric avian taxa (e.g.

Klicka et al. 2011), and environmental instability has been suggested to generate adaptive diversity (Damasceno et al. 2014).

Although ENM-based approaches to identifying putative refugia during the glacial maxima are widely used (reviewed by Alvarado-Serrano and Knowles 2014; Maguire et al. 2015; Nogues-Bravo 2009; Svenning et al. 2011), climatic conditions are not the only factor necessary for the subsistence of the species, especially if essential ecological associations are missing (Anderson in press; Svenning et al. 2011). Despite the potential that fossil pollen data has for building an understanding of past range shifts in species tied to a particular forest type, those data are often used only as a validation of climate-based hindcasts of the plants themselves (e.g. McGuire and Davis 2013; Yannic et al. 2014), and their predictive capacity to track changes in species distributions has been underutilized (Maguire et al. 2015).

Although biotic interactions have been shown to likely shape species' ranges at continental scales (e.g. Chapter 2 in this dissertation; Araújo and Rozenfeld 2014; Wisz et al. 2013), studies that include these interactions in their predictions of shifts in species distributions across times or space remain scarce (but see review in Anderson in press). When projecting ENMs to the LGM, paleo-pollen data provide the

opportunity to complement widely-used climatic reconstructions (i.e., via GCMs) with an independently-derived approximation of the vegetational composition in the past (Maguire et al. 2015; Nieto-Lugilde et al. 2015). Importantly, richness in palynological deposits has been shown to be a limited proxy for inferring plant richness (Goring et al. 2013), due to both biological differences in rates of production and transportation of pollen among plant species (Goring et al. 2013; Jackson and Lyford 1999) and artefacts related to pollen preservation, taxonomic identification, and temporal determination of the pollen record (Jackson and Lyford 1999; McGuire and Davis 2013). These challenges notwithstanding, congruence in spatial and temporal turnover of pollen and plant species has been reported (e.g. Nieto-Lugilde et al. 2015), and the use of a functional-trait aggregation of taxa, as well as broad spatial and geographical units, is likely to minimize these biases (Goring et al. 2013).

Here, I examine the biogeographical history of the New World warbler genus *Oreothlypis* in North America. I test Mengel's model by examining the three key aspects of his hypothesis: timing of diversification, ecological associations, and species' distributions during the glacial maxima. First, I constructed a time-calibrated phylogeny of all named taxa (phylospecies) in this group by sampling multiple individuals within each taxon. Based on this chronogram, I identify groups of taxa that diverged during the

Pleistocene and thus whose diversification was potentially affected by glacial cycles. I then test whether associations with climatic conditions and vegetation-types (based on palynological data) were conserved within each group, or whether these closely related phylospecies exhibited niche divergence. Finally, I build Ecological Niche Models based on climatic and palynological data independently for each taxon and project them to reconstructed conditions at the LGM, with the palynological data being used as an independent set of predictive variables rather than simply as a validation of climatically derived models. I then identify refugia as those areas with suitable vegetational composition and climatic conditions. Furthermore, if these resulting refugia are congruent with those hypothesized for other taxa, it will allow the reconstruction of the probable vicariance events and as well as Pleistocene climatic and vegetational changes that promoted speciation in this group.

3.2. METHODS

3.2.1. Phylogenetic and Time Tree Analyses

The genus *Oreothlypis* (sensu Lovette et al. 2010) includes a total of ten named taxa (phylospecies) in North America that are diagnosable based on morphological characteristics (Curson 2010; Curson et al. 1994; Lovette et al. 2010). Four of them – *O. crissalis*, *O. luciae*, *O. peregrina* and *O. virginia* – are equivalent to monotypic species. The remainder of the phylospecies have been traditionally included in two species: *O. celata,* which encompasses four subspecies (*O. c. celata*, *O. c. lutescens*, *O. c. orestera* and *O. c. sordida*), and *O. ruficapilla,* which includes two subspecies (*O. r ruficapilla* and *O. r. ridgwayi*). I sampled multiple individuals of the each phylospecies for two mtDNA loci: NADH dehydrogenase 2 (ND2) and cytochrome *b* (Cyt-*b*) following previously described protocols in Chapter 1 of this dissertation and Rabosky and Lovette (2008a) for a total of 41 individuals. Seven individuals of *O. gutturalis* and *O. superciliosa*, which are Neotropical forms of this genus and together are the sister to the monophyletic North American group (Lovette et al. 2010), were included as outgroups. Sequences for *O. crissalis* were obtained from GenBank (Accession numbers: GU932418 and GU93213).

For these individuals, I assembled and edited a total of 2148 bp for Cyt-*b* and ND2 using Geneious 6.1 (Kearse et al. 2012) and aligned them with Muscle (Edgar 2004). To understand the relationships among phylospecies and the timing of their divergence, I estimated a time-calibrated ultrametric tree in BEAST 1.8.2 (Drummond et al. 2006) in which the monophyly of taxa was not enforced to confirm whether the taxonomic delimitation od *Oreothlypis* concurs a mtDNA-based phylogeny. Site and clock models were estimated independently for each locus, but only one tree was estimated for mtDNA. Nucleotide substitution models were determined using jModeltest (Posada 2008) and were run under the HKY+G and TN93+G models for cty-*b* and ND2, respectively. A lognormal relaxed molecular clock was calculated for both loci, and a substitution rate of 1.45% per million years was fixed for ND2 (Lerner et al. 2011). I implemented BEAST 1.8.2 for a total of a hundred million generations on the CIPRES online portal (Miller et al. 2010) and discarded 10% of the runs as burn-in.

3.2.2. Locality Data and Study Area

Locality data for each phylospecies were obtained and curated following the methods in Chapter 2. Observations were based on e-Bird records

(Sullivan et al. 2009) that were observed during two months of the breeding season (June 15th to August 15th) and that were within 100 km of the widely accepted breeding distribution of each species (www.natureserve.org; Ridgely et al. 2007). Because e-Bird localities (Sullivan et al. 2009) and breeding distributions (Ridgely et al. 2007) were only recorded to the species level, I assigned each locality to the subspecies level for *O. celata* based on maps from Gilbert et al. (2010).

Similarly, I defined taxon-specific study areas from which environmental data would be drawn for ENMs and niche similarity tests (detailed description in Chapter 2). These areas were identified by including the known breeding distribution of each taxon (Ridgely et al. 2007) and a 500 Km buffer around it. Second, to control for the possible effect of biogeographical history and interspecific competition, environmental data from areas in which closely related taxa occur were excluded. Because of the coastal distribution of *O. c. lutescens*, only a small fraction of the buffered area around its distribution included environmental data, so in this case a 650 Km buffer was used. To control for sampling bias in e-Bird data, background localities were drawn from the study areas defined above proportionally to the sampling based on the entire eBird dataset for the same season as the occurrence data (Chapter 2 in this dissertation;

Phillips et al. 2009). Data manipulation and analyses were performed using the *raster* (Hijmans 2015) package in R 3.1.3 (R Core Team 2014).

3.2.3. Environmental Variables

Eight climatic variables (Hijmans et al. 2005) and 14 plant functional-group layers (based on palynological data; Williams et al. 2004) were used to quantify climatic and biotic aspects of the observed niche of each phylospecies. I used reconstructions of these sets of variables to estimate environmental conditions during the last glacial maximum (LGM; 21 Ka). Climatic conditions were based on WorldClim-bioclimatic variables (Hijmans et al. 2005) under three Global Circulation Models: The Community Climate System Model (CCSM4; Gent et al. 2011), Model for Interdisciplinary Research on Climate's Earth System Model (MIROC-ESM; Watanabe et al. 2011) and the Max-Planck Institute's Earth System Model (MPI-ESM; Stevens et al. 2013). Vegetational composition was derived from palynological fossil data in which the relative abundances of pollen taxa were estimated for intervals of 1000 years from the present to 21 Ka (Williams et al. 2004) and further classified into functional groups (Sanín and Anderson 2016; Williams et al. 1998); layers between 18 Ka and 21 Ka were considered to reflect LGM conditions.

3.2.4. Ecological Niche Divergence

To quantify the environmental divergence among phylospecies within the *celata*- and *ruficapilla* groups I performed two complementary analyses. First, to determine how the climatic and vegetational conditions in which taxa currently occur differ, I used discriminant function analyses (DFA). Because DFAs only describe the observed variation among taxa, I tested whether these differences were significant when the environmental conditions available for each taxon is accounted for by running pairwise niche similarity tests in ecological space (Broennimann et al. 2012).

For the discriminant function analyses, the values for cells in which each species was present were extracted. Four datasets were defined to analyze the climatic and palynological conditions for each species group independently. These datasets were then standardized (subtracting the mean and dividing by the standard deviation) and input as the independent variables in a linear discriminant analysis in which phylospecies were used as *a priori* categories. To interpret differentiation in ecological space, the resulting discriminant functions were subsequently correlated with the standardized environmental variables.

To test whether the quantified observed niche differences detected on the DFAs could be explained by the geographical arrangement of each group of species alone, I used the niche similarity test based on Warren et al. (2008), but implemented in ecological space (Broennimann et al. 2012). This test contrasts an empirically estimated measure of similarity (Schoener's D; Schoener 1968) between two species to multiple iterations of D calculated from randomly drawn points from environmental conditions available to each taxon (from species-specific study areas). D ranges from 0 (niches completely different) to 1 (niches identical). Species pairs for which D is significantly smaller than multiple iterations calculated from their respective background points are interpreted as displaying statistically significant niche differences accounting for the environmental dissimilarities between the areas available to the two species.

Importantly, this approach to niche-similarity tests, which is performed in ecological space, controls for spatial and ecological bias in presence localities, and does not require ENMs to be projected into regions under conditions that are not included in their training area (Broennimann et al. 2012). To do so, I did a principal component analyses (PCA) based on the correlation matrix for each set of standardized variables (climate and plant functional groups) including values for all cells in North America using the *prcomp* function in R 3.1.3 (R Core Team 2014). It is worth noting that

unlike DFAs, PCA scores are agnostic to taxon identity. I used the score-values for the two first components of each set of variables (climatic and pollen) to test for niche similarity (Broennimann et al. 2012; Warren et al. 2008) for all pairwise combinations of phylospecies of the genus using the R package *ecospat* (Broennimann et al. 2015). I conducted similarity tests for the first two principal components of each set of variables independently, running the model for 500 iterations of random samples from the background of each species pair.

3.2.5. Ecological Niche Models and LGM projections

Ecological Niche Models were built in MAXENT, version 3.3.3.k (Phillips et al. 2006) as implemented in the R package *dismo* (Hijmans et al. 2016). I chose settings in MAXENT following the protocol described in Chapter 2 using the R package ENMeval (Muscarella et al. 2014), in which the settings selected for Maxent models were based on those resulting in the smallest AICs and best transferability in terms of delta-AUC. Despite differences in intensity of the glaciations (Ehlers and Gibbard 2004), reconstructed distributions during the LGM provide a general proxy of the distributional shifts of biota during other glacial maxima, and current potential distributions should be roughly equivalent to past interglacials. Independent ENMs based on climatic and palynological variables (see

above) were then projected to LGM reconstructions of climate (CCSM4, MIROC and MPI) and vegetation composition (based on palynological record between 18Ka and 21K) without constraining the response of the models outside the training ranges of each variable (i.e. not clamping; Elith et al. 2011). To evaluate to what extent suitability patterns projected by ENMs were affected by extrapolation into non-analogous environments, I quantified areas in the continent in which the at least one variable was outside its training range.

A consideration not often taken into account in ENMs is the effect of modeling the ecological niche of a species when the latter encompasses infraspecific taxonomic variation (Hällfors et al. 2016). Moreover, local adaptation among populations can compromise the transferability of the models to different times (Hampe 2004) by violating the assumption of stationarity of the model (Murphy and Lovett-Doust 2007; Radosavljevic and Anderson 2014). To examine the effect of taxonomic delimitation on ENMs, I built models for each phylospecies independently and compared them to models made for four more inclusive polytypic taxa (defined by phylogenetic relationships and current taxonomic treatment). The first two groupings were made based on phylogenetic information generated here: one including the western phylospecies of the *ruficapilla*-group (*O. r. ridgwayi*, *O. luciae*, and *O. virginiae*) and the other including *O. c. orestera*

and *O. c. lutescens,* which are not distinguishable using mtDNA. The other two were defined by the polytypic species *O. ruficapilla* (which includes two subspecies) and *O. celata* (which includes four).

For each of the models, I quantified the number of parameters used by Maxent as a measure of complexity (Warren and Seifert 2011). It is worth noting that model selection based on the lowest AIC (see above) penalizes parameter-rich ENMs (Muscarella et al. 2014; Warren and Seifert 2011). I additionally calculated an omission rate metric (using the "10% training omission" threshold, OR10) metric to compare monotypic and multi-taxa model performance and transferability using geographically independent bins to partition training and testing data (Fielding and Bell 2002; Muscarella et al. 2014; Peterson et al. 2011). This metric calculates the proportion of test localities with suitability values below the 10% training-suitability threshold. Its value is expected to be 0.10, so larger values indicate that ENMs built with the training data predict presences in the testing dataset less adequately than those with OR10 closer to 0.10.

3.3. RESULTS

3.3.1. Phylogenetic and Time Tree Analyses

Using multiple individuals for all named taxa (phylospecies) of *Oreothlypis*, the mtDNA Maximum Clade Credibility (MCC) tree from BEAST (Fig. 3.2) resulted, with one exception, in well-supported groups. Individuals from two morphologically distinct taxa (*O. celata lutescens* and *O. c. orestera*) were co-mingled into a single clade with short internal branches, suggesting that the divergence time of these forms was too recent to be reflected as separate reciprocally monophyletic groups in mtDNA. Although deeper nodes in the MCC tree are not strongly supported by mtDNA, the topology of this tree is congruent with a previous multi-locus phylogenetic hypothesis for all parulids (Lovette et al. 2010) in which most of the nodes are well supported.

Branching times in the phylogeny placed a Late Pliocene ancestor of *Oreothlypis* in North America around 3.59 Ma (95% CI: 2.63 – 4.58Ma). At this point, the first species to diverge from the group was *O. peregrina*, a species specialized to northern boreal forests, with the other extant taxa of the group diversifying more recently. I identified two groups of taxa whose radiations were likely affected by glacial cycles of the last million years: (1)

the *celata*-group (Fig. 3.1A) including all taxa currently recognized as subspecies of *O. celata*: *O. c. celata*, *O. c. orestera, O. c. lutescens* and *O. c. sordida*; and (2) the *ruficapilla*-group (Fig. 3.1B), which includes *O. ruficapilla ruficapilla*, *O. r. ridgwayi*, *O. virginiae* and *O. luciae*.

The *celata*-group's estimated crown age was 0.35 Ma (0.23 – 0.48Ma), and it was composed of three well-supported clades. The first one corresponded to individuals of *O. c. sordida*, distributed in coastal southern California. Next followed a clade in which individuals of *O. c. lutescens* (distributed west of the Rocky Mountains from northern California to the Gulf of Alaska) were mixed together with individuals of *O. c. orestera* (distributed in the Rocky Mountains). Lastly, individuals of *O. c. celata*, found across northern North America from Alaska to eastern Quebec, formed a monophyletic group. Internodes at the base of the clade were short, suggesting a rapid radiation of the group, resulting in relationships among these clades being poorly resolved.

The estimated crown age for the *ruficapilla*-group was older: 0.84 Ma (0.61 – 1.09Ma). In this case, each phylospecies in the group w robustly supported, but as was the case for the *celata-group*, the relationships among phylospecies were not clear. I found support for *O. luciae* and *O. virginiae*, both of which are distributed in the US southwestern highlands,

to be sister taxa. In turn, they were sister to O. *ruficapilla ridgwayi*, distributed in the northern US Rocky Mountains. This relationship makes the Nashville warbler biospeces paraphyletic, but it is poorly supported by mtDNA; thus if O. *r. ruficapilla* and *O. r. ridgwayi* are instead sister-taxa, they would represent a disjunct East-West taxon.

3.3.2. Ecological niche divergence

The linear discriminant analyses recovered similar patterns of observed ecological occupation in the *celata* and *ruficapilla* groups. Relative to other species within the group, the northern forms (*O. c. celata* and *O. r. ruficapilla*) are distributed in areas with lower overall temperatures and higher temperature seasonality (Fig. 3.3A and 3.4A). Similarly, they also occur in coniferous forests in which the plant pollen composition had a comparatively higher presence of the “boreal summer green” and “shrubs” functional groups than other *Oreothlypis* taxa. Environmental conditions on both sides of the Rockies were characterized by differences precipitation-related variables. Specifically, western forms (*O. c. lutescens* and *O. r. ridgwayi*) were in areas with higher precipitation, whereas the eastern forms (*O. c. orestera* and *O. virginiae*) occurred in drier and more seasonal environments (Fig. 3.3B and 3.4B). The similarities in separation along climatic variables that these two species pairs display were not

completely reflected in the forest types in which they occur. In particular *O. virginiae,* which is distributed further south than *O. c. orestera,* is specialized in piñon-juniper and oak woodlands, which is reflected by the high frequency of the “warm temperature summer green” functional group in its breeding localities (Fig. 3.6B-C). Lastly, the southernmost forms (*O. luciae* and *O. c. sordida*) were distributed in warm and dry climates (Fig. 3.3C and 3.4B-C) and were the species that occurred in forest with the least presence of conifers.

Consistent with niche differentiation, species of the same clade (*celata* or *ruficapilla* group) had in general significantly divergent niches (Table 3.2 and 3.3) when controlling for the availability of environmental conditions and taking into account both sampling bias and differences in background areas. The first two principal components of the PCA analyses for the climatic and palynological data explained 79.2% and 81.0% of the variation for each set of variables, respectively. Phylospecies within the *celata* and *ruficapilla* groups showed different preferences in environmental space as described by the first two components of climate (Fig. 3.S2A and B) and pollen (Fig. 3.S2C and D). Niche divergence was on average stronger among species of the *celata*-group for both climatic and pollen principal components (mean: -0.40 range: -0.03 – -0.80) than for the *ruficapilla*-group (mean: -0.23 range: 0.34 – -0.72).

3.3.3. Ecological Niche Models and LGM projections

In terms of transferability, ENMs for individual phylospecies performed better than ENMs made for lumped polytypic taxa (Table 3.3). This was likely due to the environmental differentiation of each phylo-taxon (see above). When applying spatially-independent evaluation metrics ('block' method in Muscarella et al. 2014), ENMs of polytypic taxa predicted test occurrences less accurately (OR10 range 0.17 – 0.44; Table 3.3) than single-taxon models did (OR10 range 0.07 – 0.20). Thus, if multiple phylo-taxa were modeled together, ENMs trained in a section of the range of the taxon were not able to predict presence localities in other areas where the group was distributed. Additionally, when data were pooled together, ENMs tended to be parameter-rich (Table 3.3). Because of the better transferability across space in the present, models built with phylospecies are likely more appropriate for projections into past environments.

Climate-based models were broadly congruent when projected onto reconstructions from the three different Global Circulation Models (GCM) for the LGM (Figs. 3.S3 and 3.S4). For all species, areas estimated to be climatically suitable were more widespread than those estimated to be suitable by pollen-based ENMs. I defined areas to be suitable during the

LGM as those in which at least one GCM predicted climatic suitability and were also estimated to be biotically suitable in any palynological reconstruction between 18Ka and 21Ka (Fig. 3.1B and 3.D). Because of the scarcity of palynological data in the southern areas of North America, the overlap of climatic and pollen-based projections could not be estimated for the southwestern-most phylospecies (*O. c. sordida* and *O. luciae)*. For these taxa, the Baja California peninsula and northeastern Mexico were climatically suitable, but coverage of pollen layers in those areas was lacking. For these two species, none of the climatically suitable areas for which pollen data was present were biotically suitable. For all other phylospecies, suitable areas were predicted to be smaller in the past, and were located south of their current distributions (Fig 3.1). Importantly, because ENMs do not produce a direct estimate of a species' past distribution (rather, they estimate the areas that were environmentally suitable), is it important to note that eastern areas estimated as suitable for *O. c. lutescens* and *O. c. ridgwayi* (Fig. 3.1B) were not likely to be accessible to them, and therefore, were probably not part of their past range.

The most dramatic expansions during the last deglaciation were inferred for species whose current distributions were covered by glaciers at the LGM (*O. c. celata* and *O. r. ruficapilla*; green in Fig. 3.1). ENMs of these

two species projected to the LGM predicted suitable areas in the eastern USA, particularly the Appalachians for *O. r. ruficapilla*. Beringia was predicted as suitable for *O. c. celata* by climate (Fig. 3.S3A) and pollen (Fig. 3.S3B); however, suitable areas in Alaska had little overlap for these two datasets. Furthermore, Beringia represented areas of non-analogous pollen composition for all species examined. *O. c. lutescens* and *O. r ridgwayi* are currently distributed north of the Sierra Nevada in coastal areas, the Cascades and the western slope of the Rocky Mountains; these phylospecies were predicted to be more restricted to coastal distributions (orange in Fig. 3.1B and D). Analogously, *O. c. orestera* and *O. virginiae* contracted their ranges within the mountains (red in Fig. 3.1). These range shifts resulted in phylospecies being more isolated from each other than they are currently.

3.4. DISCUSSION

Based on the molecular phylogeny (Fig. 3.2), this analysis was focused on two groups of taxa: the *ruficapilla*-group and the *celata*-group that originated approximately 0.84Ma and 0.35Ma, respectively, and were strongly supported by either mtDNA or multi-loci nuclear data (Lovette et al. 2010). During the Quaternary, continental masses were located in their present configuration, and no major geological event other than the glacial cycles took place. Thus, assuming allopatry as a necessary step of speciation, the origin of these *Oreothlypis* wood-warblers was likely promoted by climate-driven vicariance events.

Divergence within the two focal groups is consistent with geographical and temporal patterns found by other phylogeographical studies in the region (Roberts and Hamann 2015; Shafer et al. 2010; Weir and Schluter 2004). Importantly, in *Oreothlypis* all phylospecies have been recognized as morphologically distinct (Curson 2010; Curson et al. 1994). In most cases, mtDNA recovered reciprocally monophyletic phylospecies. However, *O. c. lutescens* and *O. c. orestera* are not distinguishable based on mtDNA; yet these two forms are morphologically distinct, the former being significantly smaller and yellower than the other phylospecies of the group (Curson et al. 1994). Another wood-warbler, the Yellow-rumped warbler complex

(*Setophaga coronata*), has a similar distribution and exhibits the same phylogenetic pattern as *O. c. lutescens* and *O. c. orestera*. The inability to distinguish these morphologically distinct taxa based on mtDNA has been attributed to either recent divergence (Milá et al. 2007) or potential hybrid speciation (Brelsford et al. 2011). Whichever hypothesis is correct, the taxa of this complex have been shown to have regions in their genome in which divergence has been likely promoted by selection (Toews et al. 2016).

In addition to morphological and molecular differentiation, the results support divergence in climatic preferences (Table 3.1) as well as in the forest types in which these phylospecies occur (Table 3.2). Environmental differentiation in *Oreothlypis* follows the same pattern as other groups in which taxa that have traditionally been classified as one species display climatic divergence (e.g. Dowell and Hekkala 2016; Raxworthy et al. 2007; Takahashi et al. 2014). This is the first study to quantify that these climatic differences are reflected in the vegetation composition as well. Although tests for niche similarity do account for differences in available conditions, only the realized niche can be measured through correlative approaches, and thus limited inferences about the evolution of the fundamental niche can be made (Araújo and Peterson 2012; Boucher et al. 2014). Multiple studies suggest that the fundamental niches (i.e. all potentially suitable

tolerances) of closely related species are more similar than expected based on the localities in which they occur (Araújo et al. 2013 and references therein). Whether or not these niche differences in *Oreothlypis* can be directly ascribed to evolutionary changes in their fundamental niche, it is in line with multiple studies in which fast niche changes in a group have been found to be positively correlated with diversification rates (Kozak and Wiens 2010a; Smith and Donoghue 2010; Wiens et al. 2006). In summary, the present results suggest that both climatic and biotic associations contributed to the origin and maintenance of the spatial structuring of *Oreothlypis* in North America.

Niche divergence among closely related taxa also has implications for ecological niche modeling. Models for phylospecies had better performance than those in which multiple subspecific taxa were pooled together, which generally resulted in more complex over-fit ENMs (Table 3). This result is likely because of the heterogeneity of environmental conditions in which phylospecies occur (Figs 3.3 – 3.6). These differences violate the assumption of stationarity for polytypic taxa across their geographical range (Murphy and Lovett-Doust 2007; Radosavljevic and Anderson 2014). Non-stationarity would then generate parameter-rich relationships between environmental variables and the occurrence of lumped taxa, which are likely to over-fit the data (Merow et al. 2014),

resulting in an over-all accurate prediction of the present distribution of the species (e.g. *O. ruficapilla* Fig. 3.3G-H) but likely underestimate suitability when the model is projected in time or space (Merow et al. 2014). Alternatively, modeling together phylotaxa that are locally adapted would predict environments as being suitable when they are not necessarily so for populations in other parts the range (Fitzpatrick and Keller 2015; Hällfors et al. 2016; Hampe 2004). In such cases, ENMs overestimate the areas that are suitable outside the species' range (Fig. 3.3), producing projections of suitability dissimilar to those of subspecies projected independently (Hällfors et al. 2016).

ENMs based on climate data predicted more areas to be suitable during the LGM than did pollen-based models; this agrees with the idea that factors other than climate, such as dispersal limitations and community composition, also contribute to the turnover of vegetation during the last deglaciation (Blois et al. 2013a). Additionally, a large extent of the continent during the LGM had environmental conditions (based on both climate and pollen) that were not analogous to those used to train the ENMs (dark gray on Figs. 3.S3 and 3.S4). These areas represent conditions outside the present realized niche of these species, but whether or not these areas were suitable cannot be determined with correlative approaches (Araújo and Peterson 2012; Peterson et al. 2011).

Additionally, accuracy of these predictions depends on the assumption that the relationship between pollen and vegetation composition has been stationary during the last deglaciation. Unstable atmospheric conditions (Jackson and Lyford 1999) and differential pollen production as well as heterogeneous dispersal of pollen across plant species (Birks and Birks 2000; Goring et al. 2013) might represent a violation of this assumption. Thus, the examination of macro-fossils (Birks and Birks 2000) could confirm the suitability of areas proposed as refugia in this study.

ENM projections estimated a more restricted and isolated distribution for all phylospecies in comparison to their present distributions. Patterns in *Oreothlypis* coincide with other studies of Pleistocene refugia in North America (e.g. Chávez et al. 2014). Furthermore, areas identified as climatically and biotically suitable in western North America coincide with proposed refugia for multiple species of trees based on genetic, climatic and fossil data (Roberts and Hamann 2015). Specifically, *O. c. celata,* which is found in boreal forest, was likely isolated in Beringia, whereas *O. r. ruficapilla,* which occurs in mixed forests, was restricted to the Appalachians. This is consistent with the pattern found in black bears, in which populations located in areas glaciated during the LGM were hypothesized to have persisted in either a Beringian or southeastern refugium (Puckett et al. 2015). Southwestern forms (*O. c. sordida* and *O.*

luciae) presumably moved south into Baja California, which has been suggested as a climatically stable area for other taxa (e.g. Zink et al. 2013). Finally, species pairs distributed in the coastal ranges (*O. c. lutescens* and *O. r. ridgwayi*) and the Rocky Mountains (*O. c. orestera* and *O. virginiae*) contracted their ranges to the coast and the interior of the mountains, respectively. This contraction into isolated refugia resulted in allopatry, and has been proposed to have occurred in other groups such as the American pika (Galbreath et al. 2010).

On the whole, these patterns are consistent with Mengel's model in which an ancestor, broadly distributed during interglacial times, had its range fragmented during colder periods, followed by specialization to conditions in those fragments. In this system, detection of significant niche shifts in taxa that originated within the last two glacial cycles favors Mengel's model over others in which diversification is hypothesized to be a consequence of environmentally neutral fragmentation and population dynamics (Avise and Walker 1998; Haffer 1969; Mayr 1963). A major question that arises from the rapid switch in the environmental niche and dramatic range shifts of *Oreothlypis* is to what extent the LGM has "overprinted" or obscured prior biogeographic and environmental histories. However, fossil data from North American rodents imply that such range shifts were constrained to large-scale areas of endemism (Riddle 1998),

and thus at this scale, the relationship between the areas and lineage histories has not been erased by the last deglaciation.

3.4.1. Future Directions

While these results are broadly congruent with those expected from Mengel's model, they also bring attention to the fact that linking particular cladogenetic events to a specific glacial cycle is likely not possible for *Oreothlypis* given the uncertainty around divergence times estimated with mtDNA and past environmental reconstructions. Particularly, if species underwent significant niche evolution throughout the last deglaciation, reconstructions of areas that are currently environmentally suitable are less likely to reflect areas in which the species were indeed distributed (Nogues-Bravo 2009; Pearson and Dawson 2003). Although pitfalls of hindcasting species distributions are widely acknowledged (Araújo and Peterson 2012; Peterson and Anamza 2015), an approach to surmount these limitations have not yet been developed. This paper suggests that *Oreothlypis* would be an ideal system to develop a framework in which niche evolution and shifts in geographical distributions are modeled simultaneously, as these processes are interlinked. Additionally, the application of multi-locus data (Smith et al. 2013a; Toews et al. 2016) to this system offers the potential to decrease the temporal uncertainty of

diversification events. Moreover, the inclusion of community data on plant macro-fossils (Birks and Birks 2000; Maguire et al. 2015) would result in a more accurate characterization of the forest-types in which this group occurred, ultimately providing a better understanding of speciation in this group.

3.5. TABLES

Table 3.1. Pairwise niche similarity test for climate variables for *Oreothlypis* wood warblers. Values are the difference of the empirical Schoener's D (calculated in ecological space; Table 3.1S) and the average of 1000 comparisons of random localities drawn from each species' background data for PC1 (under the diagonal) and PC2 (above the diagonal). Negative numbers mean niches are more divergent than expected by the species' backgrounds, and positive numbers mean niches are more similar than expected by their backgrounds. Bold values are significantly ($p < 0.05$) different from 0.

	O. c. celata	*O. c. orestera*	*O. c. lutescens*	*O. c. sordida*	*O. viginiae*	*O. luciae*	*O. r. ruficapilla*	*O. peregrina*	*O. r. ridgwayi*
O. c. celata		-0.0229	**-0.2729**	**-0.2787**	**0.1223**	**0.4328**	**-0.2388**	**-0.2639**	**0.0570**
O. c. orestera	**-0.2173**		**-0.4465**	**-0.3762**	**0.0782**	-0.0079	**-0.1629**	**0.1574**	-0.0259
O. c. lutescens	**-0.7588**	**-0.4200**		**-0.6725**	0.0306	**-0.5332**	**0.2706**	**-0.1873**	**-0.1712**
O. c. sordida	**-0.5053**	**-0.7970**	**-0.7675**		**-0.5040**	-0.1420	**-0.7089**	-0.0335	**-0.5873**
O. viginiae	**-0.2481**	**-0.1061**	**-0.4242**	**-0.4973**		**-0.7165**	**0.3377**	**0.1737**	0.0676
O. luciae	**-0.4240**	**-0.3405**	**-0.4229**	**-0.3170**	**-0.2954**		**-0.3376**	**0.2761**	**-0.2632**
O. r. ruficapilla	**-0.3870**	-0.0461	-0.0583	**-0.4181**	**-0.1232**	-0.0840		-0.0105	**-0.0882**
O. peregrina	**-0.1029**	**-0.1637**	**-0.6092**	**-0.5658**	-0.0142	**-0.2866**	**-0.1440**		**0.1111**
O. r. ridgwayi	**-0.4038**	**-0.2568**	**-0.2988**	**-0.6909**	-0.0163	-0.0675	**0.2698**	**-0.1769**	

Table 3.2. Pairwise niche similarity test for pollen variables for *Oreothlypis* wood warblers. Values are the difference of the empirical Schoener's D (calculated in ecological space; Table 3.2S) and the average of 1000 comparisons of random localities drawn from each species' background data for PC1 (under the diagonal) and PC2 (above the diagonal). Negative numbers mean niches are more divergent than expected by the species' backgrounds, and positive numbers mean niches are more similar than expected by their backgrounds. Bold values are significantly ($p < 0.05$) different from 0.

	O. c. celata	*O. c. orestera*	*O. c. lutescens*	*O. c. sordida*	*O. viginiae*	*O. luciae*	*O. r. ruficapilla*	*O. peregrina*	*O. r. ridgwayi*
O. c. celata		-0.0299	**-0.1606**	**-0.3805**	**-0.2605**	**-0.4916**	**-0.1295**	**-0.0688**	**-0.1491**
O. c. orestera	**-0.1457**		**-0.1440**	**-0.5429**	**-0.4129**	**-0.6233**	**-0.2307**	-0.0231	**-0.0761**
O. c. lutescens	**-0.2549**	**-0.1105**		**-0.5366**	**-0.4694**	**-0.5292**	**-0.2445**	**-0.1223**	**-0.1488**
O. c. sordida	**-0.6857**	**-0.5773**	**-0.4191**		-0.1647	**-0.2916**	**-0.2308**	**-0.3892**	**-0.5225**
O. viginiae	**-0.2286**	**-0.2204**	0.0048	-0.0945		**-0.4763**	-0.0663	**-0.2804**	**-0.5114**
O. luciae	**-0.4617**	**-0.5079**	**-0.1982**	-0.1808	**-0.1508**		-0.4513	**-0.5557**	**-0.6647**
O. r. ruficapilla	0.0843	**-0.4115**	0.0544	**-0.6568**	**-0.3769**	**-0.4565**		**-0.1360**	**-0.3053**
O. peregrina	**-0.1938**	-0.0743	-0.0668	**-0.4020**	**0.0015**	**-0.2479**	**-0.0887**		**-0.1314**
O. r. ridgwayi	**-0.2115**	**-0.1544**	-0.0371	**-0.4082**	0.0335	**-0.2887**	**-0.3687**	**0.0560**	

Table 3.3. Summary statistics and Maxent settings of the best-performing ENMs (lowest AIC score) for models of *Oreothlypis* wood warblers built for single taxa and multi-taxon groups. Letters in feature classes stand for: L = Linear, Q = Quadratic, H = Hinge, P = Product, and T = Threshold. R. Mul. stands for "Regularization Multiplier, OR for the omission rate metric (using the "10% training omission" threshold, see text),"and Param. for number of parameters. .

	Climate-based models				Pollen-based models			
Taxon	**Features**	**R. Mul.**	**OR10**	**Param.**	**Features**	**R. Mul.**	**OR10**	**Param.**
O. c. celata	LQHPT	2.5	0.07	29	LQH	3	0.08	44
O. c. orestera	LQH	4.5	0.14	17	LQHPT	2	0.14	13
O. c. lutescens	LQHP	1	0.15	59	LQH	1.5	0.12	21
O. c. sordida	LQ	1	0.11	7	LQH	3	0.13	8
O. c. orestera and *O. c. lutescens*	LQH	4.5	0.18	16	H	5	0.17	23
O. celata (four subspecies)	LQHPT	2.5	0.31	51	LQHPT	1	0.44	86
O. r. ruficapilla	LQHPT	2.5	0.14	33	H	4	0.14	46
O. r. ridgwayi	LQH	1	0.12	54	LQHP	2.5	0.20	47
O. luciae	LQ	4.5	0.19	9	L	1	0.22	8
O. virginiae	LQ	4.5	0.20	10	LQ	3	0.21	11
O. r. ridgwayi, *O. virginiae* and *O. luciae*	H	5	0.22	16	LQ	1.5	0.25	20
O. ruficapilla (two subspecies)	LQH	1.5	0.19	83	LQHPT	1	0.24	109

3.6. FIGURES

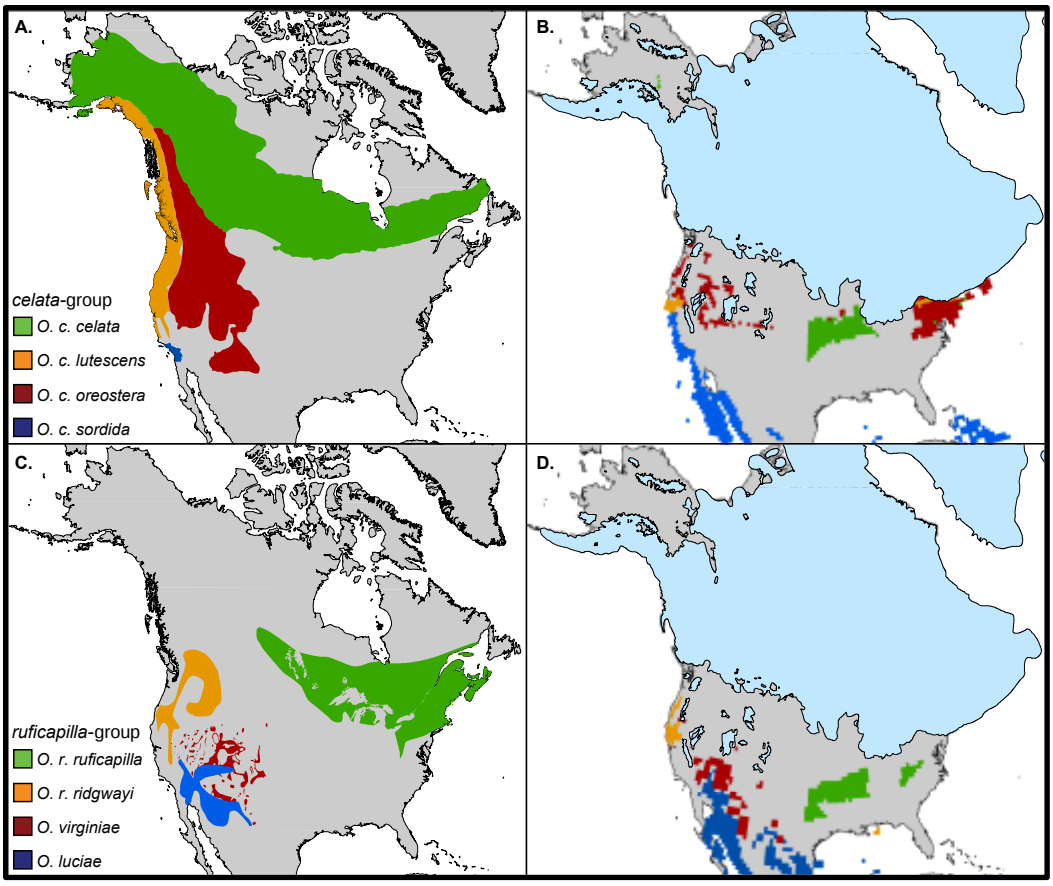

Figure 3.1. Left: Maps of suitable breeding conditions for the taxa in (A) the *celata*-group and (C) the *ruficapilla*-group of *Oreothlypis* wood warblers. Right: projected areas suitable during the LGM for (B) the *celata*-group and (D) the *ruficapilla*-group. These are areas in which projections of at least one climatic model and one palynological one (between 18Ka and 21Ka) predict suitability. Because of the lack of palynological data in Southwestern North America, regions indicated in B and D for *O. c. sordida* and *O. luciae* (blue areas) are areas of climatic suitability.

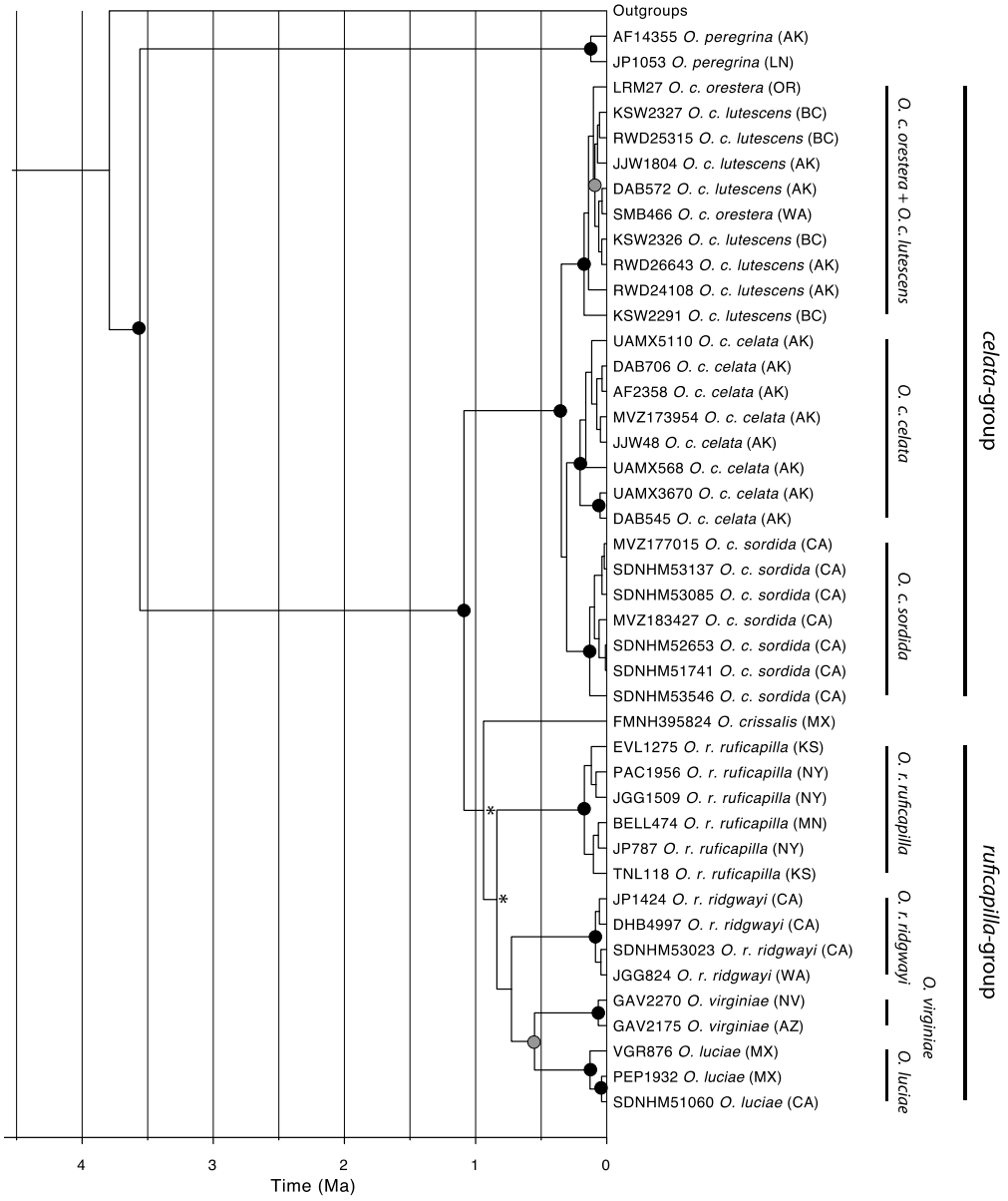

Figure 3.2. Bayesian Maximum Credibility Tree of all North American individuals sampled for of the *Oreothlypis* warblers. Black and gray circles represent nodes with posterior probabilities equal to or greater than 0.99 and 0.95 respectively. Stars indicate nodes which are not strongly

supported by the mtDNA dataset but are (pp >0.99) in a multi-locus analysis of all parulids (Lovette et al., 2010).

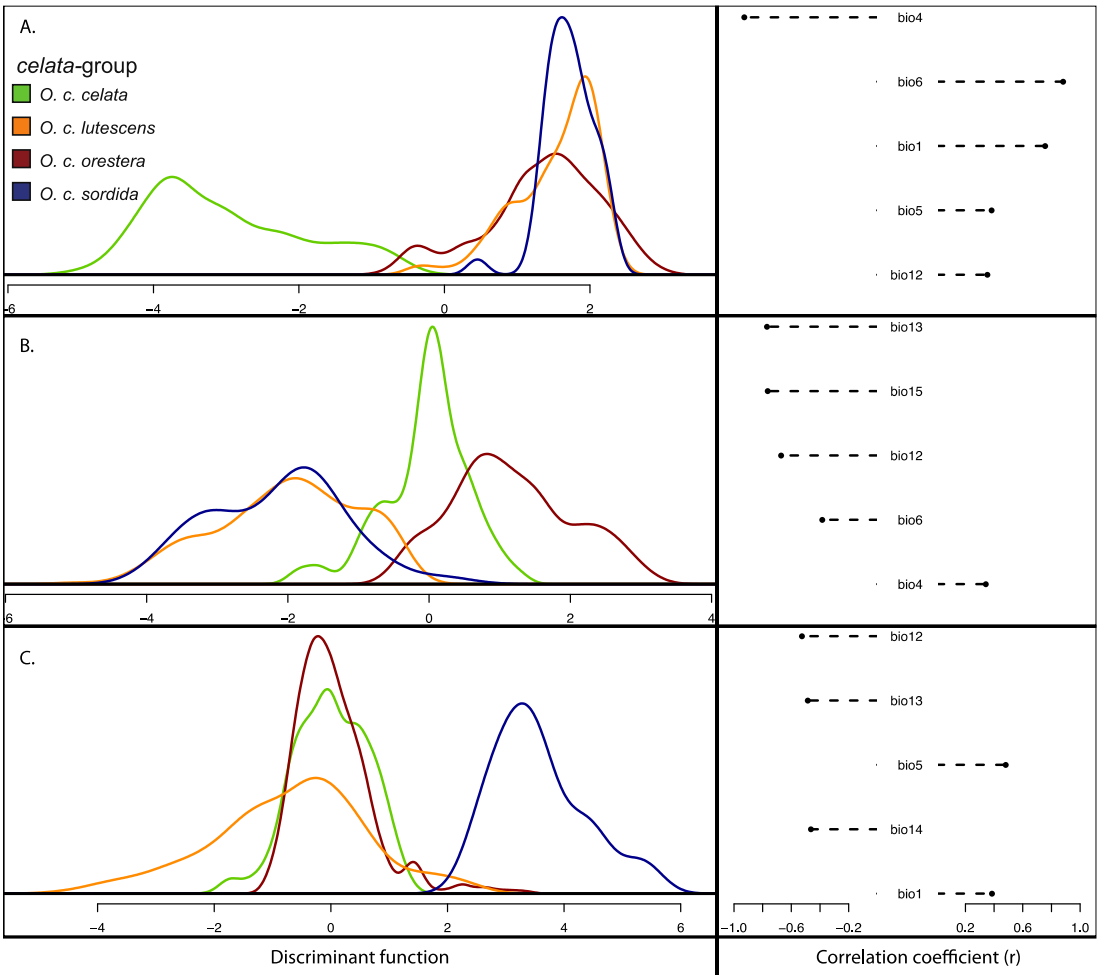

Figure 3.3. Divergence in ecological space of the taxa in the *ruficapilla*-group based on a linear discriminant analysis of climatic variables. Curves in the left panels represent the values of each taxon for the three discriminant functions (A to C). Panels in the right display the five most correlated climatic variables for each function and the direction and magnitude of each correlation. Variable abbreviations follow Table 3.1S.

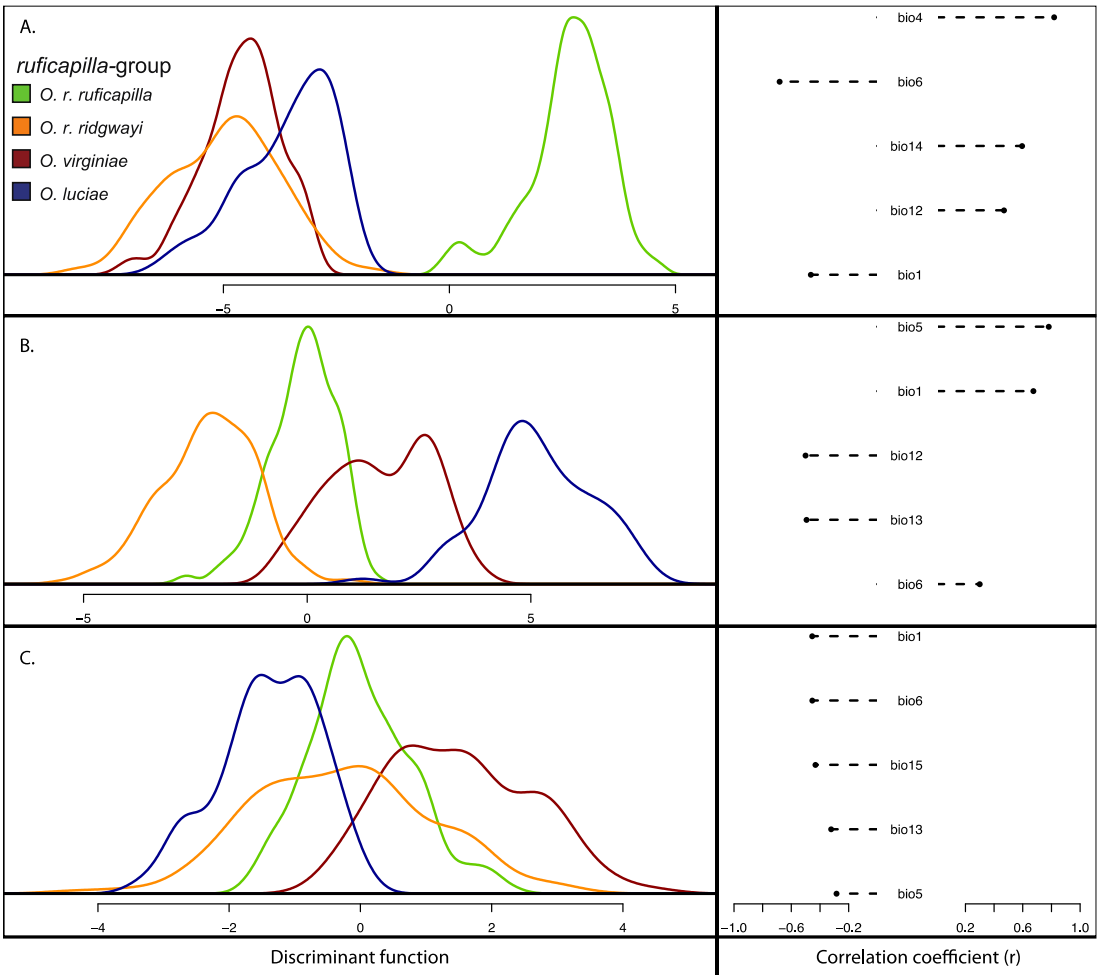

Figure 3.4. Divergence in ecological space of the taxa in the *celata*-group based on a linear discriminant analysis of climatic variables. Curves in the left panels represent the values of each taxon for the three discriminant functions (A to C). Panels in the right display the five most correlated climatic variables for each function and the direction and magnitude of each correlation. Variable abbreviations follow Table 3.1S.

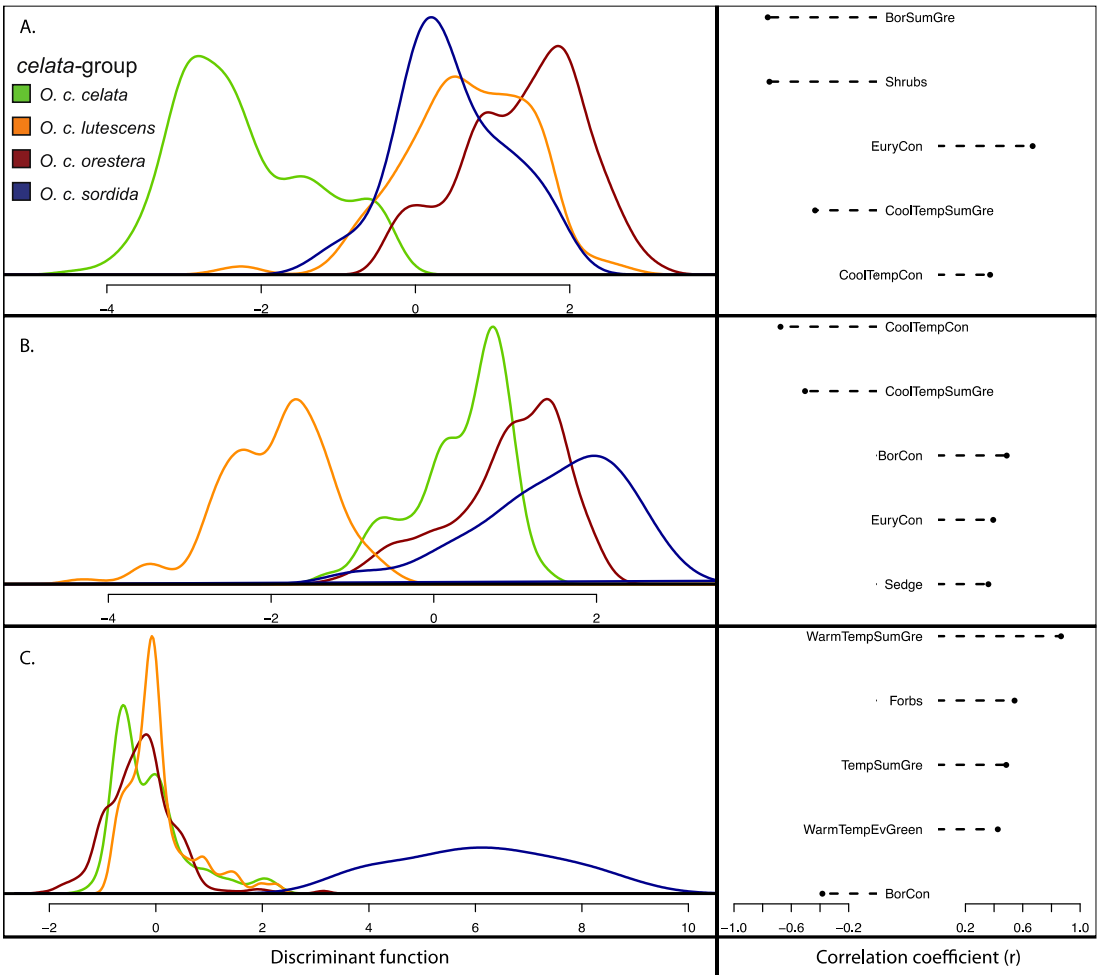

Figure 3.5. Divergence in ecological space of the taxa in the *ruficapilla*-group based on a linear discriminant analysis of palynological variables. Curves in the left panels represent the values of each taxon for the three discriminant functions (A to C). Panels in the right display the five most correlated climatic variables for each function and the direction and magnitude of each correlation. Variable abbreviations follow Table 3.1S.

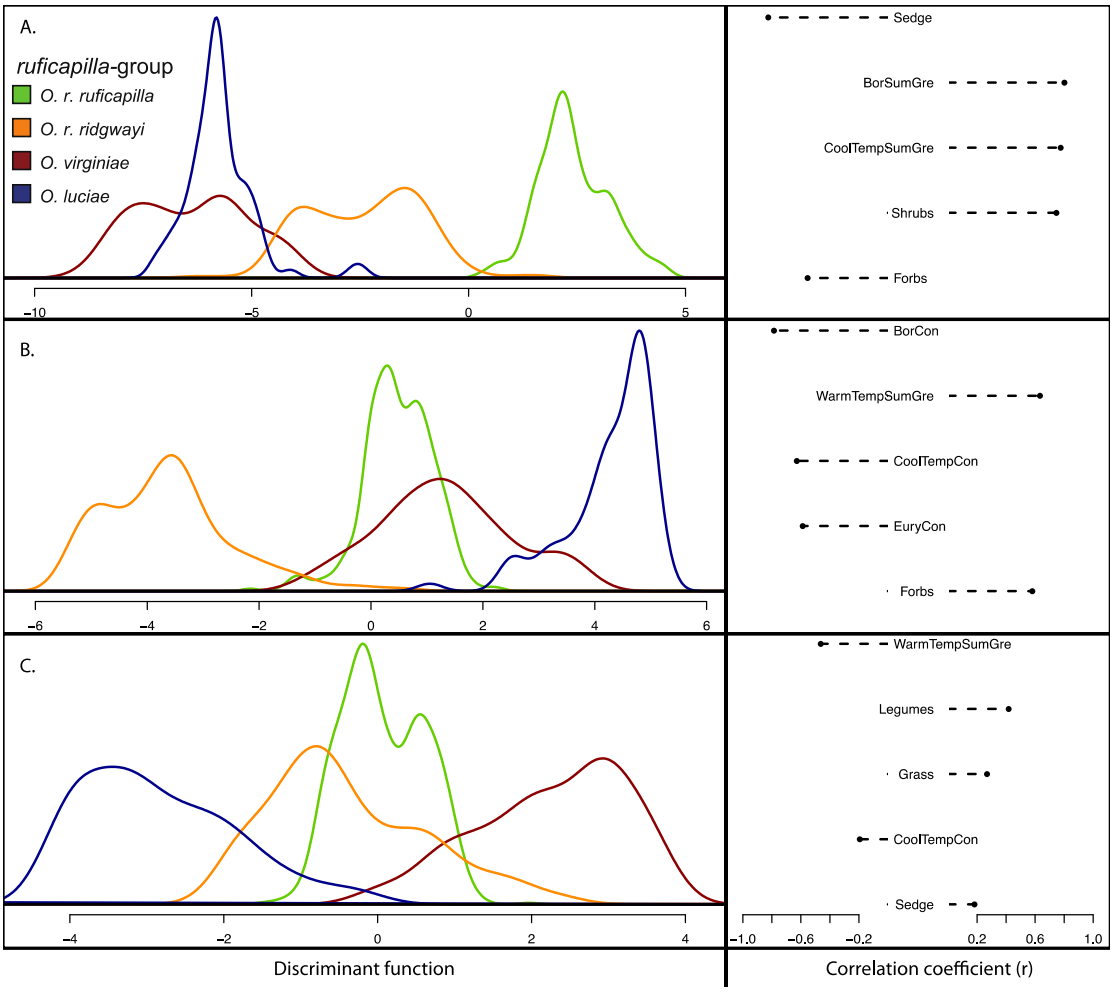

Figure 3.6. Divergence in ecological space of the taxa in the *celata*-group based on a linear discriminant analysis of palynological variables. Curves in the left panels represent the values of each taxon for the three discriminant functions (A to C). Panels in the right display the five most correlated climatic variables for each function and the direction and magnitude of each correlation. Variable abbreviations follow Table 3.1S.

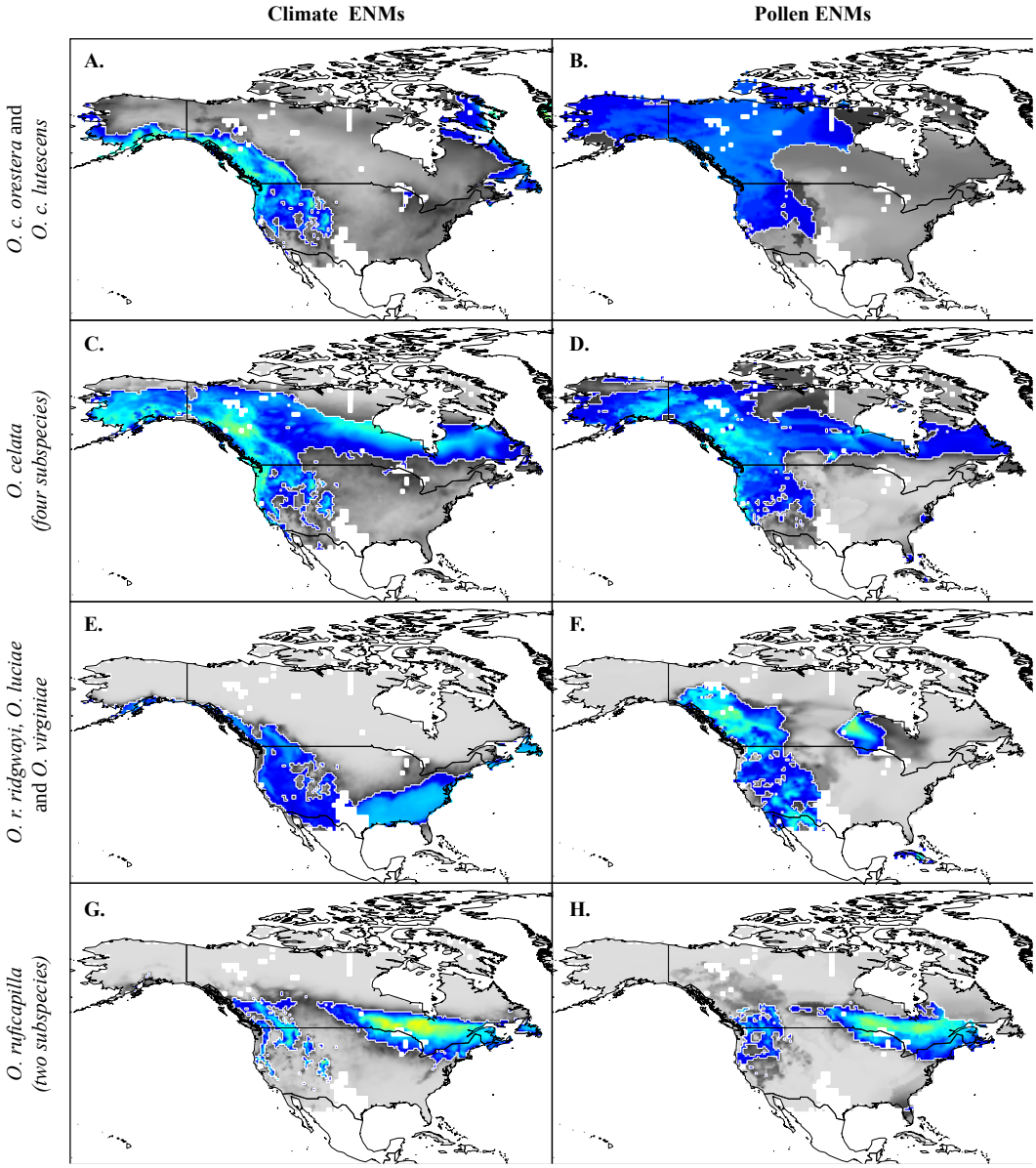

Figure 3.7. ENMs of *Oreothlypis* wood warblers based on climatic (left) and palynological (right) data built simultaneously for polytypic taxa. Light to dark grays represent relative suitability below the respective 10% omission rate thresholds, and cold to warm colors show increasing suitability above those thresholds.

3.7. ANNEXES

Table 3.S1: Biotic and abiotic variables included in as environmental predictors.

Table 3.S2: Pairwise niche similarity for climate variables for North American wood warblers of the genus *Oreothlypis*. Values are the Schoener's D (calculated in ecological space) for PC1 (under the diagonal) and PC2 (above the diagonal). D ranges from 0 (niches completely different) to 1 (niches identical).

Table 3.S3: Pairwise niche similarity for pollen variables for North American wood warblers of the genus *Oreothlypis*. Values are the Schoener's D (calculated in ecological space) for PC1 (under the diagonal) and PC2 (above the diagonal). D ranges from 0 (niches completely different) to 1 (niches identical).

Figure 3.S1: Areas projected to be suitable by ENMs for each phylospecies of the *celata*-group (left panels) and the *ruficapilla*-group (right panels) of *Oreothlypis* wood warblers. Suitability is defined by a 10% omission rate threshold. Shades of red represent support of a single ENM

projection of climatic or pollen data (light red) or support of both EMNs (dark red).

Figure 3.S2. Distribution in ecological space of (left) the *ruficapilla*-group and (right) the *celata*-group of *Oreothlypis* wood warblers. Values in top panels represent climatic space (PC1 and PC2 of bioclimatic variables on x and y-axes respectively) while bottom panels are related to vegetation composition (PC1 and PC2 of palynological functional groups on x and y-axes respectively). Each point represents the value of a cell sampled, and lines connect them with the centroid for each taxon. For reference, the location in environmental space for five National Parks are highlighted in black.

Figure 3.S3: Areas projected to be suitable by ENMs for each phylospecies of the *celata*-group of *Oreothlypis* wood warblers during the LGM. Projections are based on climatic (left panels) and palynological (right panels) data. Suitability is defined by a 10% omission rate threshold. Blue and light gray represent suitable and not suitable areas with conditions analogous to those sampled in the calibration region of each ENM. Red (suitable) and dark gray (not suitable) represent projections to non-analogous environments.

Figure 3.S4: Areas projected to be suitable by ENMs for each phylospecies of the *ruficapilla*-group of *Oreothlypis* wood warblers during the LGM. Projections are based on climatic (left panels) and palynological (right panels) data. Suitability is defined by a 10% omission rate threshold. Blue and light gray represent suitable and not suitable areas with conditions analogous to those sampled in the calibration region of each ENM. Red (suitable) and dark gray (not suitable) represent projections to non-analogous environments.

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